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The life system of the yellow-headed fireworm, Acleris minuta (Robinson) (Lepidoptera: Tortricidae)

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THE LIFE SYSTEM OF THE YELLOW-HEADED FIREWORM, ACLERIS MINUTA (ROBINSON) (LEPIDOPTERA: TORTRICIDAE)

Iowa State University PH.D. 1982

The life system of the yellow-headed fireworm, *Acleris minuta* (Robinson) (Lepidoptera: Tortricidae)

by

Julie C. Weatherby

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I. INTRODUCTION

A resident population of the yellow-headed fireworm, Acleris minuta (Robinson) (Lepidoptera:Tortricidae), is established in the commercial nurseries of southwestern Iowa. Mount Arbor Nursery, located in Fremont County, has suffered sporadic losses from this lepidopterous defoliator with the most recent epidemic occurring in 1973 - 1975. Concern over these recurring economic losses to the rosaceous and ericaceous plantings stimulated this research.

Prior to this work, the basic biological data on this species were limited to descriptive and fragmentary information compiled in the late 1800s and early 1900s. Therefore, this study was designed to use laboratory and field populations to 1) develop a comprehensive biology, 2) analyze the population dynamics, and 3) begin the synthesis of a life system model. By meeting these objectives, the potential exists through the mechanics of computer simulation to describe, predict, and manage A. minuta population levels.

Species within the genus Acleris have a restricted host specificity (Powell 1964). Apparently only members of the Rosaceae and Ericaceae serve as adequate host species for A. minuta, an endemic species of the cosmopolitan family Tortricidae that apparently has evolved a preference for an introduced host species, Malus pumila Mill. (Chapman 1973). Apple is the primary host and feeding is confined to the buds and the leaves (Chapman and Lienk 1971). In the late nineteenth century, damage attributed to the yellow-headed fireworm was reported from New Jersey and

from several midwestern states. Reports of economic population levels within apple nurseries in Illinois and Iowa are scattered throughout the literature of this period, with special references made to the years 1863, 1870, and 1871 (Webster 1909). Attention was again drawn to this apple pest in 1883 and 1884 in the "14th Report of the State Entomologist of Illinois" (Weed 1889). Historical accounts can be found (Smith 1884, Weed 1889, Stedman 1896) with the most complete work appearing in 1909 entitled "The Lesser Apple Leaf Folder" (Webster 1909). Injurious infestations have been reported on plum nursery stock in Ohio as well as on cranberry in the eastern United States (Webster 1909). Webster (1909) listed pear, wild rose, high-bush whortleberry, hucklebery, and blueberry as additional host species, while MacKay (1962) in her treatment of the larval Tortricinae, made reference to specimens collected from peach. Kalmia angustifolia L. was added later (Ferguson 1975) to this list.

Uniformly, the literature dealing with the seasonal life history of A. minuta has referred to 3 broods in latitudes similar to Iowa and the possibility of 2 broods in areas further north (Smith 1884, Weed 1889, Stedman 1896, Webster 1909, Chapman and Lienk 1971). Smith (1884) stated that in New Jersey the gray moth (overwintering color morph) was found flying by the middle of April followed by the 1st summer moth flight in early June, the 2nd summer moth flight in August, and the winter or gray moth flight in October. This gray form was described as a separate species, Tortrix cinderella, by Riley in 1872. Dimorphism within the species was not officially recognized until 1884 when Fernald synonymized

the gray form with the orange form (Obraztsov 1963). Weed (1889), recognizing the fragmentary nature of the current data, stated that "I believe that they are sufficient to establish the fact of the dimorphism and the 3 broodedness of Teras minuta upon apple." Razowski (1966) in his treatise on the "World Fauna of the Tortricini" concentrated primarily on the taxonomy of the species based upon adult characteristics, specifically the male genitalia. Obraztsov (1963) compiled a complete synonomy for Acleris minuta (Robinson) and Acleris minuta (Robinson) form cinderella Riley. Powell (1964), while naming a new species, speculated that Acleris paracinderella Powell "is very close to the otherwise unique Acleris minuta (Robinson) and paracinderella may be a western race of minuta."

A variation in the ovipositional site preference exists between the color morphs (Webster 1909). The winter moth deposits eggs in crevices on the bark while the summer moth exclusively oviposits on both the top and bottom surfaces of apple leaves (Webster 1909). Eggs are deposited preferentially on "terminal twigs or shoots where growth is rapid and the leaves young" (Stedman 1896).

Several brief behavioral observations of the larvae are contained in Webster's article (1909). MacKay (1962), concentrating on larval taxonomy, has compiled setal and morphological maps based on a total of 7 preserved specimens. The pupa is described uniformly in several sources with emphasis placed on the unusually large anterior protuberance (Smith 1884, Weed 1889, Stedman 1896, Webster 1909, Chapman and Lienk 1971).

Descriptive life histories, such as that compiled for the yellow-headed fireworm, do not explain adequately pest population changes

associated with modern agriculture. Agriculturalists and entomologists have become increasingly aware of the losses attributable to insect pests. The elimination of crop diversity associated with self-sufficient farming, the cultivation and planting of vast acreages to a single crop species, and the dependency upon pesticides has increased the pest status of many insect species. While it is still necessary to have detailed descriptive information concerning pest species, applied entomologists are directing much of their research toward the explanation of the behavior of the agroecosystem. The life history of a pest species only can be described adequately when the interrelationships between the pest and its environment are considered.

Within the last twenty years, applied entomologists have begun implementing systems analysis techniques, originally developed by managerial strategists, into the fields of pest management. Pest management has been defined as "the reduction of pest problems by actions selected after the life systems of the pest are understood and the ecological as well as economic consequences of the actions have been predicted, as accurately as possible, to be in the best interest of mankind" (Rabb 1970). This definition implies that predictions of ecological and economic consequences resulting from control actions upon a complex biological system can be made and understood. To aid and to improve predictive capabilities, entomologists are becoming increasingly dependent upon systems analysis.

Systems analysis has been described as a process that can be broken down into 3 broad phases. Phase I pertains to the construction of models

based upon data and theories that describe the behavior of the system; Phase II encompasses the validation of the models; and Phase III concerns the utilization of the systems models to predict the systems behavior under "normal and imposed conditions" (Berryman and Pienaar 1974).

Models of the life systems of many of the major economic pests, including the tobacco budworm (Stinner et al. 1974b, Hartstack et al. 1976), the corn earworm (Stinner et al. 1974b, Hartstack et al. 1976, Logan et al. 1979), the cereal leaf beetle (Helgesen and Haynes 1972, Gutierrez et al. 1974, Tummala et al. 1975), the alfalfa weevil (Ruesink 1976), the boll weevil (Jones 1975, Gutierrez et al. 1979), the European corn borer (Loewer et al. 1973), the Douglas-fir tussock moth (Campbell 1977), and the southern pine beetle (Foltz et al. 1976, Coulson et al. 1976, 1979) are in various stages of construction and phases of reconstruction. These pioneering efforts in dynamic systems analysis have been of a descriptive nature (Ruesink 1976). The challenge currently facing systems scientists is to transform these descriptive models, utilizing the methods of computer simulation and optimization, into tools for the evaluation of management strategies (Shoemaker 1976). "Simulation, ..., allows us to test the effects of experimental manipulation of system parameters on abstractions of the real system without the risk and cost involved in real-life experimentation in the field and laboratory" (Berryman and Pienaar 1974).

Fundamental to an agroecosystem simulation is the construction of realistic and accurate life system models (Streifer and Istock 1973). Valid simulations result in accurate prediction of the state of the real

system; however, accurate prediction must result from realistic models that describe the behavior of the natural system (Ruesink 1976).

The construction of systems models for pest species generally has consisted of an insect population dynamics model coupled with a host plant growth, development, and yield model. "An insect cannot be adequately modeled without concurrently modeling the plant. The plant regulates the insect's temperature, food supply and reproduction sites, thereby regulating its development rate and fecundity" (DeMichele 1975). In 1974, the United States Department of Agriculture, with congressional appropriations, began the USDA Expanded Douglas-Fir Tussock Moth Research and Development Program. One of the objectives of this program was to "assemble an integrated pest management system for the Douglas-fir tussock moth" (Anon. 1978). Within 5 years, concentrated efforts had been made to realize this objective by constructing the Douglas-Fir Pest Management System. Serving as an excellent example of the current utilization of systems analysis in pest management, the stand prognosis model and the Douglas-fir tussock moth outbreak model are combined, supplying interactive input into a socio-economic model, resulting in management decisions. As a result of this combined research effort, a forest manager soon should be able to predict the probable outcome of a Douglas-fir tussock moth outbreak and the effects of management decisions dealing with such an outbreak.

Research conducted during 1976 - 1980 has clarified the life history of A. minuta. Quantifiable interactions between the fireworm and its host plants, the commercial varieties of apple, have been investigated. A

schematic graph of the life system of A. minuta (Figure 1) has been formulated based on the results of this research. Four subsystems compose the life system.

Subsystem I - Fecundity and Oviposition

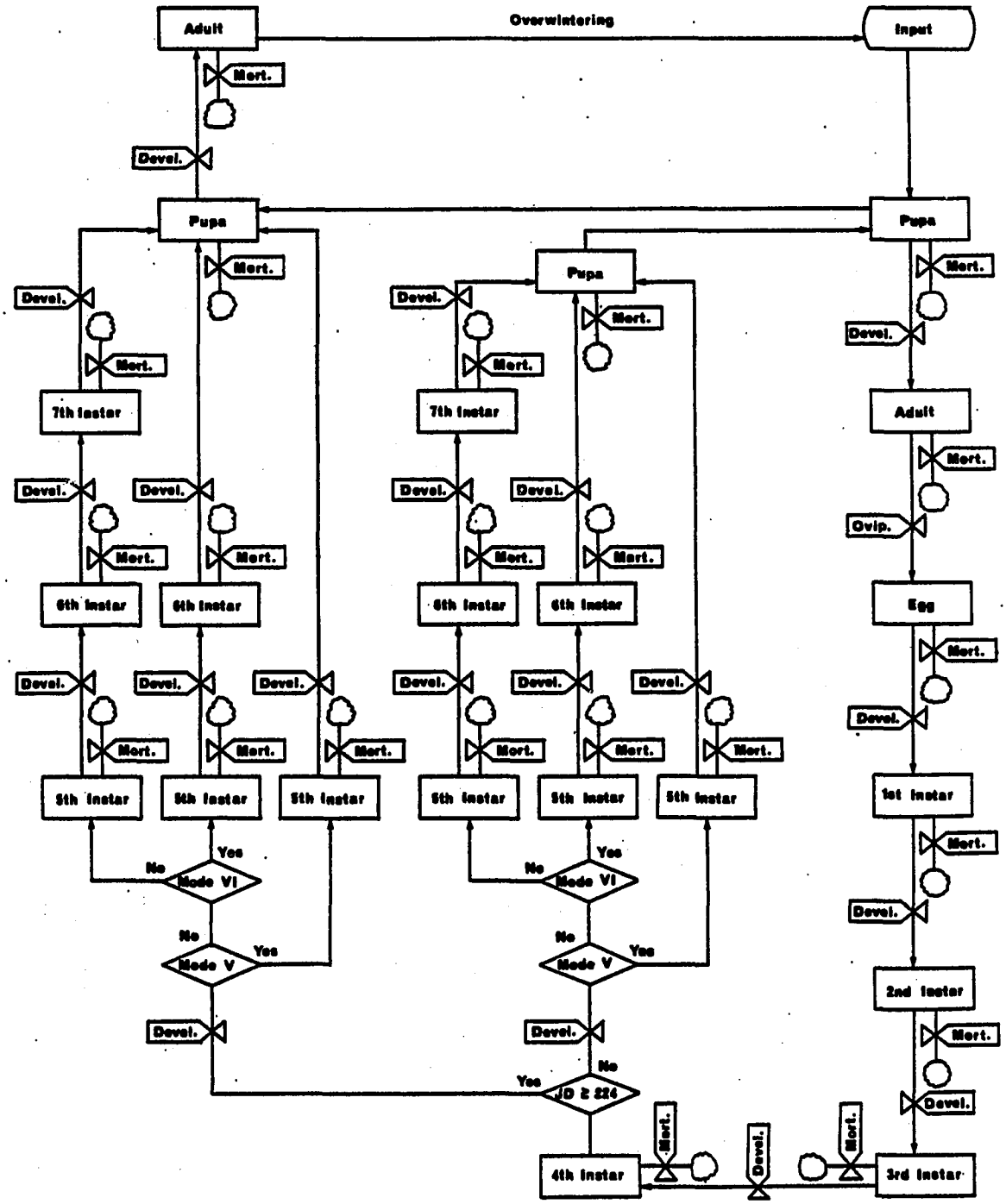
Subsystem II - Development of Larval Instars 1 - 4

Subsystem III - Development of Larval Instars 5, 6, and 7 Under Summer and Winter Photoperiods

Subsystem IV - Overwintering

Many of the subsystems can be divided into components. A component has been described "as the largest coherent subset which when combined captures the essence of the problem" (Coulman et al. 1972). Models constructed for the major insect pests generally have classified life stages as components (Coulman et al. 1972). Because of the fact that life stages within the A. minuta model are distinct and subjected to specific parameters, each life stage will be considered a component. Each component must be described by a mathematical model that results from a stimulus/response interaction between the exogenous input variables, the state variables, the component parameters, and the endogenous output variables (Coulman et al. 1972). The exogenous input variables are generally the driving force, i.e., degree days, that act upon the state variables, i.e., population densities, under the functional relationship established by the parameters, i.e., rate functions, to produce the endogenous output variables. The components are linked such that the output of one component becomes the input of the next. Input of a cohort of pupae into the system model results in the simulation of daily cohorts of individuals for each life stage.

Figure 1. Schematic diagram of the life system of A. minuta


Adult
Overwintering
Input
Mort.
Devel.
Pupa
Pupa
Pupa
Mort.
Devel.
Mort.
7th instar
7th instar
Adult
Devel.
Mort.
Ovip.
6th instar
6th instar
6th instar
6th instar
Egg
5th instar
5th instar
5th instar
5th instar
5th instar
5th instar
1st instar
No
Yes
Mode VI
Mode V
2nd instar
DD ≥ 224
4th instar
3rd instar

A life system approach will serve as the theme of this dissertation. The Literature Review has been divided into sections that correspond to the subsections covered in the Results and Discussion section. The Results and Discussion section will present the biological data and will develop the concepts and interrelationships used in the construction of the conceptual model of the life system of A. minuta. The conceptual model will be described in the Summary.

II. LITERATURE REVIEW

A. Adult Flights

Entomologists have encountered many logistical problems associated with sampling adult flying insects. Adaptive selection pressures have resulted in morphological and behavioral adaptations that tend to make some insects inconspicuous. It is not surprising, therefore, that attractive trapping methods such as pheromone trapping have been developed.

A pheromone has been defined as a "chemical or a mixture of chemicals that is released from an organism and that induces a response by another individual of the same species" (Shorey 1977). The presence of mating pheromones, those chemicals specifically evolved to instigate a series of behaviors terminating in copulation, have been documented quite well for lepidopterous insects. The pioneering work of Collins and Potts (1932) clearly demonstrated the attraction of males to chemicals produced by virgin females and female extracts of Lymantria dispar (L.), the gypsy moth. Tamaki (1977) has compiled a list of 70 lepidopterans from which pheromones have been identified. Approximately 39% of these identifications have been from members of the family Tortricidae.

The potential uses for sex pheromones in integrated pest management systems will not be realized until detailed aspects of the bionomics and attractancy behaviors of the pests under varying environmental conditions are understood. Successful seasonal control programs for the codling moth, Cydia pomonella (L.), have been based on interpretations of phero-

mone trap catches (Bethell et al. 1972, Madsen and Vakenti 1973). Paradis and Comeau (1972), working in southwestern Quebec, found that the number of codling moth males captured correlated well with the number of damaged apples. Madsen and Peters (1976) reported that sex pheromone catches for Archips argyrospilus (Walker) showed good correlation with population densities while MacLellan (1978), working in Nova Scotia, found no correlation between male A. argyrospilus catches and apple damage. These conflicting reports are not unusual and probably attest to the complexities associated with pheromone mediated behavior. Accurate estimates of absolute density from trap catches "will involve proper interpretations of the influence of interacting biotic and abiotic factors on mating flight behavior" (Batiste et al. 1973a). Several factors have been suggested that may determine the magnitude of codling moth pheromone trap catch (Riedl and Croft 1974). Spatial and physical characteristics of traps, such as trap design, condition of trap, and rate and concentration of pheromone release compounded with trap placement and distribution in relation to population concentrations may alter trapping efficiency. Population densities of indigenous and immigrating males, sex ratios of males to females, and age distributions of males from different populations vary throughout the periods of greatest sexual flight. In addition to these characteristics associated with trap design and populations, stereotyped behavioral patterns modified by environmental factors affect the magnitude of the daily and seasonal trap catches.

Several articles concerning the effects of exogenous environmental factors upon sexual circadian rhythms have been reviewed by Carde and

Webster (1981). The female calling behavior of many lepidopterous species has been demonstrated to follow endogenous or circadian rhythms (Carde and Roelofs 1973). Evidence exists that circadian sexual activities in Lepidoptera are entrained by environmental factors, i.e., photoperiod (Batiste et al. 1973b, Sanders and Lucuik 1975, Webb and Berisford 1978), lunar phases (Nemec 1971), adult thermoperiod (Loughner 1972), or pupal thermoperiod (Truman 1973). In theory, these free running circadian rhythms should continue on a regular schedule despite the absence of the entraining factor. "The expression and timing of these rhythms can be modified by many organisms by exogenous environmental factors" (Carde and Webster 1981). The calling behavior of Holomelina immaculata (Reakirt) is suppressed by continuous light despite the fact that the female's circadian rhythm is entrained by photoperiod (Carde and Roelofs 1973). After 48 hours of a 17-hrs. light and 7-hrs. dark regime, spruce budworm moths anticipated lights-off on the 3rd night even when held under continuous illumination (Sanders and Lucuik 1975).

A generalized pheromone mediated mating model is difficult if not impossible to describe. Adaptive selection pressures have resulted in specific efficient mating systems "temporally coordinated such that mating activities occur synchronously and under optimal conditions in a heterogeneous and variable environment" (Carde and Webster 1981).

Because of varying environmental conditions, the circadian gate occasionally occurs during periods when optimal responsiveness is physiologically impossible. Temperatures below 10°C have been shown to deter male flight. Webb and Berisford (1978), working with laboratory

held Nantucket pine tip moths, Rhyacionia frustrana (Comstock), found that 83% of the males were able to initiate flight at 15°C while only 4% flew at 10°C. Codling moth flight was limited by temperatures below 13°C and above 27°C (Batiste et al. 1973b). Under laboratory conditions, lower constant temperatures have shifted the female pheromone release and male responsiveness of Argyrotaenia velutinana (Walker) to earlier extremes of the circadian gate (Bollinger et al. 1977). Mating behaviors and temporal responsiveness vary according to complex aspects of temperature regimes, particularly the rate of temperature decrease and the temperature just prior to the flight period (Comeau et al. 1976). By correlating mean hour of activity and the evening average temperature, shifts in the red-banded leaf roller's hour of activity can be related to the temperature during the daily interval 1800-2300 hours EDST (Comeau et al. 1976). This daily temperature fluctuation results in moths flying earlier on cool days and later on warm ones. "The difference in photoperiod between spring and summer did not have any apparent relationship to the shifts in periodicity between flights" (Comeau et al. 1976). Moths experiencing a drop in temperature from 24° to 23°C two hours prior to initiation of calling commenced calling within 12 minutes of the temperature decrease while moths held at a constant 23°C advanced their periodicity of calling by only 30 minutes (Carde et al. 1975). From this research, it was concluded that the "decrease in temperature has an independent cueing effect distinct from the temperature level" (Carde et al. 1975). Both male and female mating activity periods of Trichoplusia ni (Hbn.) advanced under decreasing temperatures (Bollinger et al. 1977). In addition to

this temperature stimulated advancement in responsiveness, males reared under fluctuating temperatures (25°:15°C) "tended to be 3 to 6 times more responsive to pheromones than those maintained at the constant 25° or 15°C" (Bollinger et al. 1977). This increased responsiveness may be due to a 3 to 6 fold increase in sensitivity caused by a physiological lowering of the threshold of responsiveness for those individuals reared at a fluctuating temperature (Bollinger et al. 1977).

Light intensity, wind velocity, and humidity are cited as exogenous environmental factors that have an influence on pheromone trapping efficiency and timing. Males and females of Choristoneura fumiferana (Clem.) displayed similar levels and patterns of precopulatory activity under on/off and gradual illumination (Sanders and Luciuk 1975). Females displaying conditioned free running calling rhythms under constant illumination responded by advancing the calling period when exposed to premature dusk (decrease in intensity) (Sanders and Luciuk 1975). Webb and Berrisford (1978) reported "no apparent relationship between specific light intensities and time of first flight activity of R. frustrana on either warm or cool nights." Trichoplusia ni females reduced the duration of the calling period when exposed to wind velocities less than .3 m/sec. and above 1 m/sec. (Kaae and Shorey 1972).

Despite the sensitivity of pheromone trapping as a monitoring technique, trapping fluctuations brought about by alterations in 1) physical characteristics of the trap, 2) rate and concentration of pheromone emission, 3) distribution and age associated responsiveness of the population, and 4) stereotyped behavior patterns modified by fluctuating

environmental factors have made numerical predictions of population densities based on trap catch unreliable. Standardization of trapping techniques and schemes associated with a specific pest may remove some of the variation. Without substantial improvement, population densities predicted from pheromone trap catch will continue to introduce unacceptable error into population models for most species of insects.

Accuracy of physiological-time models in predicting the phenology of natural insect populations has improved when pheromone trapping has been used as biological reference points. Biofix I, "the date of first male codling moth or moths in the pheromone trap with no significant interruption in catch," provided an accurate estimate of first emergence (Riedl et al. 1976). Currently pheromone trapping as a tool in population modeling and integrated pest management shows promise as a timing mechanism.

B. Reproductive Rate

The net-reproductive rate for a population is the mean number of progeny contributed by each female (Price 1975). Factors that affect the net-reproductive rate include: 1) the mating efficiency, 2) the fecundity, 3) the ovipositional pattern, and 4) the adult longevity.

Little is known about the mating efficiency of field populations of tortricid species. Mating generally occurs during a 24-hour period after female emergence (Powell 1964). Most tortricid populations have a balanced sex ratio and protandry is not unusual (Powell 1964). In

addition, it appears that a single mating provides enough sperm to fertilize the eggs oviposited by an average female (Powell 1964).

Environmental factors affect the pheromone communication system (Section II. A) and the mating efficiency of many lepidopterous species. Temperature influenced the mating efficiency of C. pomonella females significantly. At 26.7°C, approximately 80% of the laboratory reared females mated while at 23.9°C the mating success rate decreased to 59% (Howell 1981). "Temperature related changes in mating frequency also have been observed in field populations of codling moths" (Howell 1981). Unusual environmental conditions, e.g., low temperatures, that temporarily prevent mating probably do not remove newly emergent tortricid females from the breeding population. Newly emergent females that do not mate during the first mating activity period can be mated successfully during subsequent activity periods (Powell 1964).

Fecundity, both realized and potential, is highly variable among females belonging to the same population. Individual fecundities for codling moth females ranged from 11 to 345 eggs per female (Howell 1981). A mean fecundity of 100 to 200 eggs per female is probably representative for species within the tribe Tortricini (Powell 1964).

For short-lived lepidopterous species, larval nutrition may be the most important factor affecting potential fecundity. Larvae reared on inferior host plants usually produce smaller pupae (Beckwith 1976, Barbosa and Greenblatt 1979), and pupal weight is highly correlated with adult fecundity (Beckwith 1976, Hough and Pimentel 1978). The mean fecundity

for Anticarsia gemmatalis Hbn., the velvetbean caterpillar, averaged 963.4 and 515.0 eggs per female when larvae fed on early vegetative and senescent soybean leaves, respectively (Moscardi et al. 1981). Larval crowding also has been shown to reduce adult fecundity (Gruys 1970, Beckwith 1976).

Natural selection pressures acting on short-lived species favor high ovipositional rates during the beginning of the ovipositional period (Price 1975). Eggs oviposited early in the reproductive period result in substantial increases in a population's capacity for increase (Andrewartha and Birch 1954). Tortricid females usually begin ovipositing on the evening following mating (Powell 1964). Stedman (1896) reported that A. minuta females oviposited over a period of 3 to 5 days.

While larval nutrition affected the fecundity and the daily ovipositional rate of the velvetbean caterpillar, the ovipositional pattern remained relatively constant (Moscardi et al. 1981). Regardless of food source, approximately "50% of the eggs were laid during the first 5 days after female emergence" (Moscardi et al. 1981).

The ovipositional pattern, on a chronological scale, for Heliothis spp. is determined by an interaction between adult longevity and temperature (Hartstack et al. 1976). The duration of the ovipositional period averaged 10 days at 32.2°C and increased to 30 days at 15.6°C (Hartstack et al. 1976). In addition to changes in the duration of the ovipositional period, lower temperature delayed peak oviposition by several days.

Based upon these findings, the net-reproductive rate for any lepidopterous species is a highly variable statistic. The realization of the

reproductive potential of a population is dependent upon the existing environmental conditions.

C. Developmental Polymorphism

At the beginning of the 20th century, several theories were postulated concerning the growth of arthropods (Brooks 1886, Dyar 1890, Przibram and Megusar 1912). These theories stated that growth followed a geometric progression. Dyar (1890) postulated that each species grows according to a characteristic constant growth factor that he calculated as the ratio of any given head capsule width to the head capsule width of the next instar. Based upon this theory, all healthy larvae of a particular species would be expected to pass through a defined number of larval stadia growing at a geometric rate characteristic of the species. Under optimal conditions, most lepidopterous larvae develop through a minimal number of instars growing at a near maximal growth rate and, therefore, "Dyar's Law" appears to apply. However, environmental conditions are seldom stable enough to support this maximum growth rate throughout the duration of larval development. "Dyar's Law" cannot explain adequately the occurrence of supernumerary instars, or developmental polymorphism (Schmidt and Lauer 1977) characteristic of many lepidopterous species (Hoskins and Craig 1935, Allegret 1964, Leonard 1970a, Scriber 1977).

Supernumerary molts may be hereditary or may be caused by inadequate nutrition and other external factors (Wigglesworth 1965). The number of larval instars of the gypsy moth varies with sex (Leonard 1970a), larval

crowding (Leonard 1968), maternal nutrition (Leonard 1970b), and food deprivation of 1st instars (Leonard 1970a). Similarly, larvae of Orgyia pseudotsugata (McDunnough), the Douglas-fir tussock moth, pupate after 4 to 6 larval stadia depending upon sex, host tree species, and age of the food source (Beckwith 1976).

Within instars, a high positive correlation exists between final larval weight of the preceding instar and head capsule width, suggesting that nutrition as expressed by larval weight is influential in the occurrence of supernumerary molts (Beck 1950). Beck (1950) experimenting with Ostrinia nubilalis (Hbn.), the European corn borer found that "the principal factor determining the width of the larval head capsule was the weight of the molting insect and not its instar number."

For all herbivorous lepidopterans, adequate larval nutrition is dependent principally upon the ingestion of nitrogen from the host plant (Soo Hoo and Fraenkel 1966a, 1966b, Taylor and Bardner 1968, Feeny 1970, Schramm 1972, Slansky and Feeny 1977). Leaves of herbaceous host plants are considered to be more nutritious than leaves of woody shrubs and trees (Whittaker 1966, Soo Hoo and Fraenkel 1966b, Fraenkel 1953). Leaves of herbaceous plants generally have a higher nitrogen content, a higher water content, and a lower non-digestible fiber content (Scriber and Feeny 1979). These differences often become more pronounced as the season progresses, particularly after woody shrubs and trees cease to put on new "flushes" of growth.

"Larvae of Pieris rapae L., the cabbage butterfly, adjust their feeding rate to maximize the rate at which they can accumulate nitrogen

and thus the rate they grow" (Slansky and Feeny 1977). Pieris rapae larvae grow as rapidly on host plants of 1.5% (dry weight nitrogen) as on plants of 4.8% (dry weight nitrogen). Therefore, the growth rate of P. rapae larvae is influenced as much by the availability of nitrogen as by the rate of consumption. When the rate of consumption increases beyond the level where nitrogen can be accumulated efficiently, larval growth will be slowed (Slansky and Feeny 1977).

Unlike forb-feeding larvae, tree-feeding larvae "are more sensitive to water content of the leaves" (Scriber and Feeny 1979). The nitrogen utilization efficiency and the nitrogen accumulation rates decreased drastically when larvae of Hyalophora cecropia (L.) fed on leaves with low water contents (Scriber 1977). Because of the decreases in nitrogen utilization efficiency and nitrogen accumulation rates, larvae fed leaves with low water content tend to grow more slowly. Most lepidopterous tree defoliators feed in the spring when nitrogen and water contents are highest and allelochemics are at the lowest concentrations (Feeny 1970). "Whether singly or in combination, nutrient content and texture factors seem to act as quantitative barriers, setting ultimate ecological limits to the growth of herbivores" (Scriber and Feeny 1979).

If growth rates vary in response to the nutritional value of the host plant and if supernumerary molts are common among lepidopterans, what factors determine the point at which larval development is terminated? Insects do not count molts (Wigglesworth 1948). The insect measures its growth rate and when this growth rate is maximal, the corpora allata (CA) are inactivated and the insect pupates. Based upon this currently

accepted theory, most lepidopterous species are not programmed to pupate after a species-specific number of instars. The works of Nijhout and Williams (1974a, 1974b) explain many of the complexities associated with the control of molting and the decision to pupate. Nijhout and Williams postulated that 2 critical larval sizes exist for Manduca sexta (L.), the tobacco hornworm (Williams 1976). The first size is a species-specific size that is assessed by the larva at ecdysis. If the larva exceeds the first critical size, the ensuing instar becomes the final instar. A larva assesses its size through stretch receptors that send nervous impluses to the brain (Nijhout 1975). As the larva grows, increased tension is placed upon the stretch receptors and the pattern of nervous impulses changes. When the stretch receptors determine that the larva has exceeded the critical size, the nervous impulses alert the neuro-hormonal system, committing the larva to pupation. The second critical size coincides with the release of the "inhibitor" that acts on the brain causing the brain to turn off the secretion of juvenile hormone (JH) by the CA. Unlike the first critical size, the second critical size is not species-specific. The second critical size is directly proportional to the first critical size. In the absence of JH, the brain is now free to secrete prothoracicotropic hormone (PTTH) that acts on the prothoracic gland controlling the secretion of ecdysone (Nijhout and Williams 1974a, 1974b). "Ecdysone activates the pupal gene-set" (Williams 1976). Many aspects of molting and metamorphosis are still mysteries. Because of the many similarities among endocrine systems of various species, it is likely that the generalized processes of molting and metamorphosis, as discovered in M. sexta, are universal, particularly among herbaceous lepidopterans.

D. Developmental Models

The principle of heat-unit accumulations particularly relating to the development of plants and poikilotherms was developed during the 18th century (Pradhan 1946). Under the principle of heat-unit accumulations, a linear relationship exists between the rate of development and temperature (Kitching 1977). Therefore, each species develops according to a thermal constant that is calculated as the product of the duration of development and the effective temperature (Davidson 1944, Pradhan 1946). When the summation of the daily effective temperatures reaches the specific thermal constant, development is completed.

At the extremes of thermal exposure, growth rates deviate from the linear relationship. The currently accepted concept is that the relationship between the rate of development and temperature is modeled more accurately by a curvilinear relationship (Kitching 1977). Both sigmoid and polynomial models have been suggested as an improvement over the previously accepted linear model (Andrewartha and Birch 1954, Stinner et al. 1974a, Logan et al. 1976, Kitching 1977, Hammond et al. 1979). Despite general agreement that the rates of development and temperatures do not follow linear relationships, utilization of linear models has continued to surface in the literature (Hughes and Gilbert 1968, Tyndale-Biscoe and Hughes 1969, Gilbert and Gutierrez 1973). Under all proposed models, the relationship between growth rates, within the median portion of the total temperature range, and temperature is linear. Development in the field under periods of favorable thermal accumulations can be described adequately by a linear relationship. Development

"during critical periods at the beginning and end of a season, and during the height of the summer" are described accurately by curvilinear relationships (Kitching 1977). The use of a linear model, particularly during periods of low temperatures could result in unacceptable error (Stinner et al. 1974a).

Most of the developmental models described previously have been constructed from data sets gathered from constant temperature laboratory rearings (Messenger and Flitters 1959). Pradhan (1946) showed that 1) at the lower temperature extremes development proceeded more rapidly under variable temperature than under equivalent constant temperature, 2) at the upper temperature extremes development was slowed under variable temperatures, and 3) in the mid-portion of the temperature range development under constant and variable temperatures proceeded at similar rates. Messenger and Flitters (1959) stated that "the acceleration or deceleration caused by exposure to variable temperatures with different diurnal ranges of fluctuations may be ascribed to one or more of the following factors: 1) ... the non-linearity of the constant temperature-velocity curve, 2) development at temperatures below the constant temperature threshold, 3) the nonequivalence of time and degree of growth at different temperatures, that is, the nonadditivity of hour-degrees, and 4) unknown factors, which may be assumed ... to be due to some inherent value of the variable temperature environment not occurring under constant temperature conditions."

Several procedures have been developed for calculating heat-unit accumulations (Lindsey and Newman 1956, Arnold 1960, Allen 1976,

Sevacherian et al. 1977). Apart from the problems associated with acquiring accurate temperature measurements, heat-unit accumulations provided only estimates of the occurrence of a designated biological event (Arnold 1960). The most accurate procedure for accumulating heat units is to measure the area under a normal daily temperature curve when the temperature exceeds the threshold for development (Arnold 1960). The applicability of this procedure is limited to research where detailed temperature records are kept. Frequently, the only temperature records available are daily maximum and minimum temperatures. Several procedures have been developed that reconstruct daily temperature curves based on maximum and minimum temperatures. One method estimates the temperature curve by triangulation between 2 consecutive minimum temperatures and the associated maximum temperature (Lindsey and Newman 1956). This approach was modified to adjust for differences between 2 consecutive minimum temperatures (Sevacherian et al. 1977). Sine curves have been suggested frequently as an adequate method for estimating the normal temperature curve (Arnold 1960, Allen 1976). The error between actual temperature accumulations and estimates based on maximum and minimum temperatures "is small enough to suggest the use of a heat-unit system based on maximum and minimum temperatures in most commercial work and some types of research" (Arnold 1960).

E. Color Morph Development

Polymorphism is common within the tribe Tortricini, and members of the genus Acleris are among the most variable of all lepidopterans (Powell

1964). Most color morphs within the genus Acleris are examples of genetic polymorphism (Powell, J. A., Department of Entomology, UCB, personal communication). Price (1975) defines genetic polymorphism as "the occurrence together in the same population of two or more discrete forms of a species in proportions greater than can be maintained by recurrent mutation alone." Unlike genetic polymorphism, seasonal polymorphism is rare among tortricids (Chapman and Lienk 1971). Seasonal polymorphism is characterized by "a marked difference in color between successive generations that can be correlated with seasonal changes in environment" (Chapman 1969). Seasonal photoperiods are the most consistent stimuli that may induce seasonal polymorphism (Chapman 1969).

F. Life Tables

The population dynamics of any species result from complex interactions between innate capacities of each member of the population and environmental constraints. These innate capacities that are described most often in terms of mean values for the population include the birth rate, the death rate, and the rate of development (Andrewartha and Birch 1954). A descriptive statistic that is used to describe the growth potential of a population with a stable age distribution under a defined environment is the innate capacity for increase (Andrewartha and Birch 1954). This statistic has been used to compare 1) the growth potentials of different populations of the same species (Orphanides and Gonzales 1971), 2) the growth potentials of populations of different species (Messenger 1964, Force 1970), and 3) the effects of variable environments

upon the growth potential of the same population (Messenger 1964, Tanigoshi et al. 1975, Herbert 1981). The data required to calculate the innate capacity for increase include an age schedule of survivorship of the female population and an age schedule of fecundity for that population (Birch 1948). This information is summarized adequately in life tables.

Life tables have been constructed to summarize the dynamics of both laboratory and natural populations. Pearl and Parker (1921) constructed the first experimental life table for an insect species, Drosophila melanogaster Meigen. Morris and Miller (1954) adapted this approach developing ecological life tables for natural insect populations. Harcourt (1969) reviewed the role of life tables in the discipline of population dynamics and the techniques required in the construction of reliable ecological life tables. Crucial to the construction of any life table is a sampling scheme that results in accurate estimates of the age specific density. For many insect species, this is a difficult task. Successive developmental stages may overlap, and a direct estimate of the number entering a stage cannot be obtained directly from a series of samples. Several methods have been used to obtain accurate age specific density estimates (Southwood 1966). The simplest method is the area-under-the-curve technique that was developed to obtain density estimates of Oscinella frit L (Southwood and Jepson 1962). The difference between the age specific densities of 2 successive stages is an estimate of the population change resulting from various factors, e.g., immigration, emigration, predation, parasitism, disease, starvation, etc. After the construction of life tables for several successive generations,

an evaluation can be made of the role each factor plays in density regulation.

Single-factor or key-factor analysis was introduced into the field of population dynamics to simplify the "multi-factor" approach of life table analysis (Morris 1959). A key factor is defined as the factor causing a degree of mortality most closely related to the changes in the population densities of successive generations (Morris 1959).

Several methods for identifying key factors have been developed (Varley and Gradwell 1960, Podoler and Rogers 1975). The Varley-Gradwell method involves a visual comparison between graphs of the total generation mortality and the mortality caused by each factor. Each single-factor mortality is expressed as a killing power (k value) that is calculated as the difference between logarithms of the population density before and after the mortality has occurred. The total generation mortality (K) is the sum of the killing power of all the mortality factors. The total generation mortality (K) and the single-factor mortalities (k) are plotted for successive generations and the graphic patterns are compared. The single-factor graph that most closely resembles the total generation graph is identified as the key factor. Podoler and Rogers (1975) developed a quantitative method that involves regressing each single-factor k value (Y axis) on the total generation K (X axis). The single-factor k value that results in "the greatest value for the slope is the key factor" (Podoler and Rogers 1975).

Frequently, life table data is used to describe the relationships between population densities and mortality rates. Mortality factors can

be classified as density dependent or density independent (Varley et al. 1973). The mortality rates of density independent factors show no relationships to population densities. A density dependent factor is directly density dependent if the factor "kills an increasing proportion of the population as the population density increases" (Varley et al. 1973). If a mortality factor consistently results in the death of fewer individuals as the population increases, the factor is classified as inversely density dependent (Varley et al. 1973). Factors that respond with a time lag to fluctuations in population densities are classified as delayed density dependent (Varley et al. 1973). Life table, key factor, and density dependent analyses are important tools used to identify factors that may explain and regulate population densities.

The population dynamics of A. minuta have not been investigated. The only mortality factors that have been identified in the literature are parasitoids (Table 1).

Table 1. Parasitoid complex identified in the literature

Current Name	Synonym	Reference
Tachinidae		
Blondelia eufitchiae (Townsend)	(= *Masicera eufitchiae*)	Webster 1909
Hemisturmia tortricis (Coq.)	(= *Phorocera tortricis*)	Aldrich and Weber 1924
	(= *Neopales tortricis*)	Weiss 1917
Nemorilla pyste (Wik.)	(= *Nemorilla maculosa*)	Franklin 1950
	(= *Nemorilla* sp.)	Webster 1909
Braconidae		
Macrocentrus delicatus Cresson		Smith 1884
		Weed 1896
		Webster 1909
Apanteles cacoecia Riley		Weed 1896
		Webster 1909
Oncophanes americanus (Weed)	(= *Clinocentrus americanus*)	Weed 1896
		Webster 1909
Ichneumonidae		
Itoplectis conquisitor (Say)		Franklin 1950
Scambus hispae (Harris)	(= *Pimpla minuta*)	Weed 1896
Chorinaeus carinatus Cresson		Webster 1909
Campoplex validus (Cresson)	(= *Limneria teratis*)	Weed 1896
Sinophorus sp.		Webster 1909
Horogenes obliteratus Cresson	(= *Limneria elegans*)	Weed 1896
		Webster 1909
Temelucha forbesi (Weed)	(= *Cremastus forbesi*)	Weed 1896
		Webster 1909
Chalcidoidea		
Brachymeria ovata (Say)	(= *Chalcis ovata*)	Webster 1909
Catolaccus aeneoviridis (Girault)	(= *Arthrolytus aeneoviridis*)	Webster 1909
Horismenus microgaster (Ashmead)	(= *Pediobioidea cyanea*)	Webster 1909
Sympiesis bimaculatipennis (Girault)	(= *Astichus bimaculati pennis*)	Webster 1909

III. MATERIALS AND METHODS

A. Adult Monitoring Studies

A series of trapping experiments initiated in 1977 was conducted in a 2 year old grafted apple nursery in Farragut, Iowa. The experimental field contained rows of three varieties of apple, Jonathan, yellow delicious, and red delicious (Figure 2). All trees used in this study were outplanted in rows on a 0.18-m (7") by 1.12-m (44") spacing, as 1 year old single grafted seedlings. In 1977 when the trapping experiments began, the trees were beginning the second growing season. The field was divided at 15.24-m (50') intervals into 26 plots such that each plot contained all 3 varieties (Figure 2). The plots were numbered consecutively from east to west. In plots 6, 11, 19, and 22, 2 trapping locations were randomized within each variety. At each trapping location, a 1.52-m (5') length of 1.91-cm (3/4") conduit was driven into the ground within the row. Two Pherocon® 1 CP traps were positioned on each pole, at a height of 0.30 m (1') and 1.22 m (4') above the ground (Figure 3). A total of 48 traps were monitored weekly throughout the growing season to provide information on seasonal adult flights.

To obtain virgin females to use in baiting the traps, first generation larvae were collected from the field during April and reared in the laboratory. Twenty-four newly emerged moths were caged individually in ventilated containers equipped with dental wick water sources (Figure 4). Each week a new set of 24 moths was transported to the field. Traps were baited by securing a caged moth within the sticky trap. At location 1,

Figure 2. Diagram of the experimental field (Farragut, Iowa)

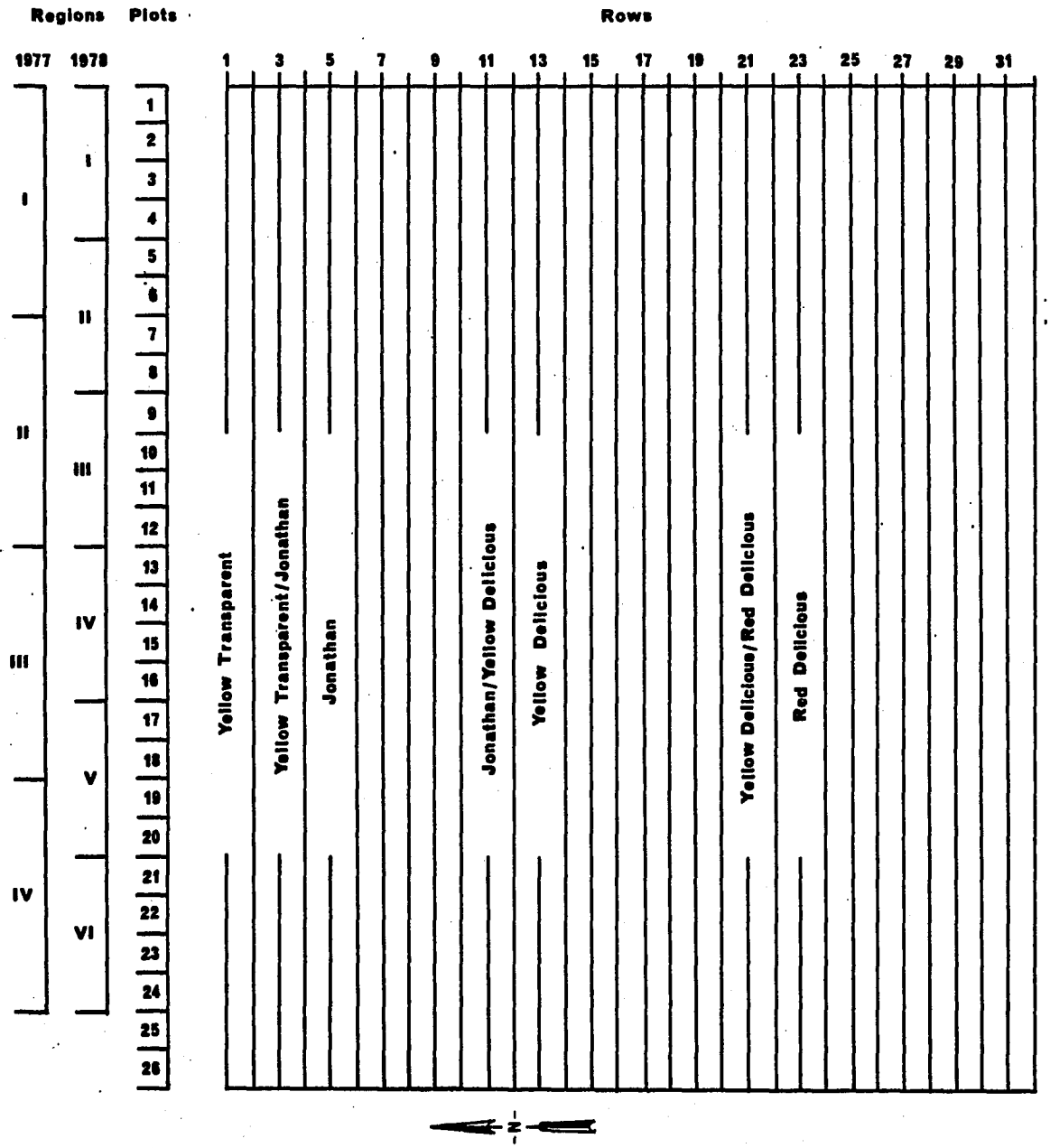

Regions
Plots
Rows
1977
1978
I
II
III
IV
V
VI
1
3
5
7
9
11
13
15
17
19
21
23
25
27
29
31
Yellow Transparent
Yellow Transparent/Jonathan
Jonathan
Jonathan/Yellow Delicious
Yellow Delicious
Yellow Delicious/Red Delicious
Red Delicious
N

Figure 3. Virgin female baited traps used to monitor seasonal adult flights

Figure 4. Virgin female baited Pherocon® 1 CP sticky trap

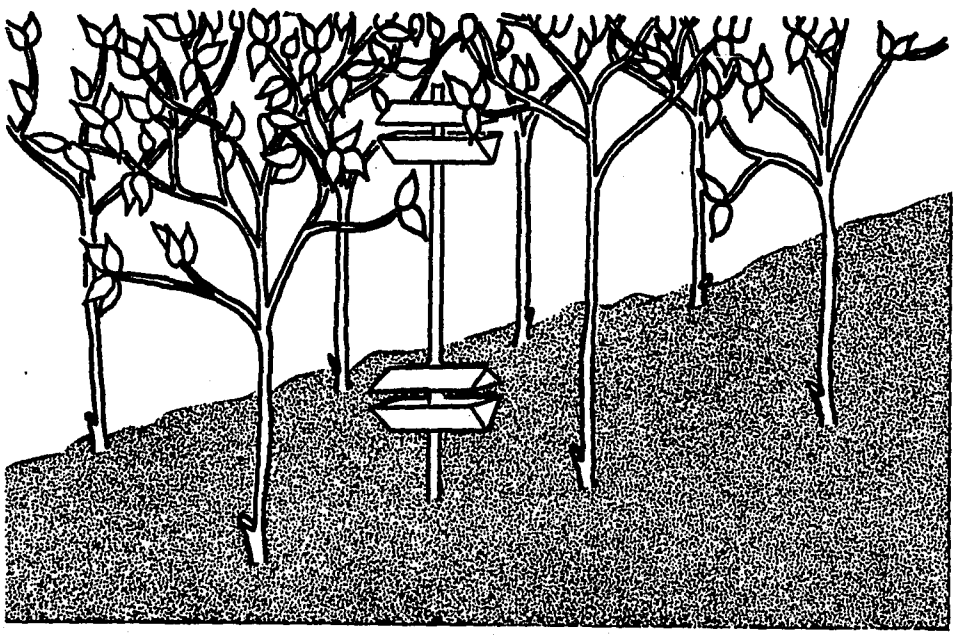


Figure 3.

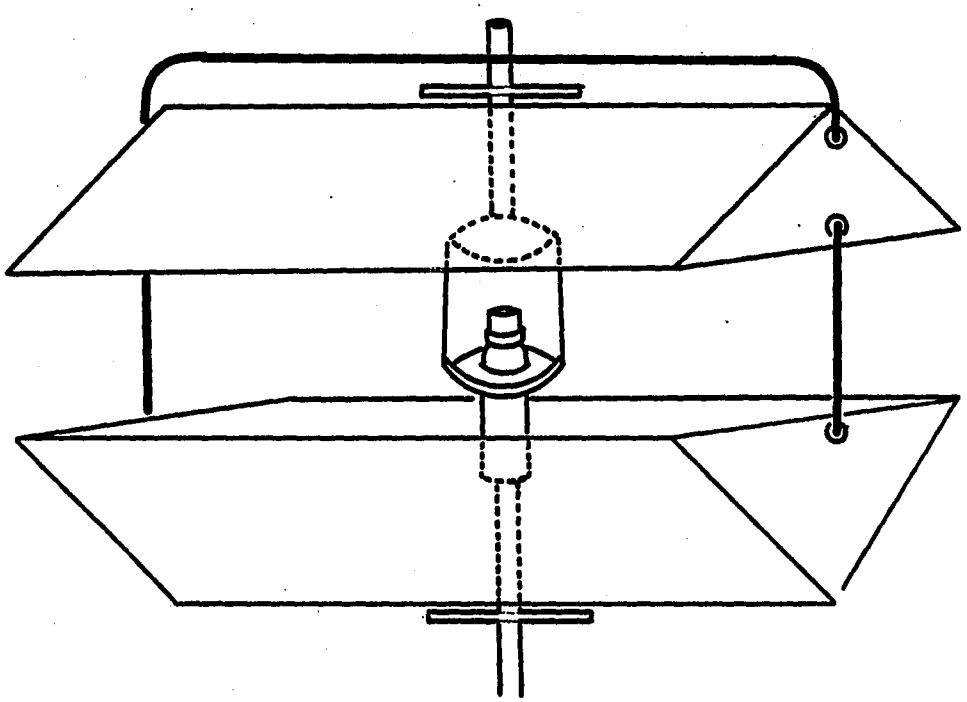


Figure 4.

within each plot and variety, only the bottom trap was baited; at location 2, the top trap was baited. Once a week, the captured moths were counted and removed from the traps.

In addition to monitoring the seasonal flight activity of the population with virgin female baited traps, an experiment was designed to determine the hours of greatest male activity. The same physical design as described previously was used in this experiment. Once an hour for 24 hours, each trap was checked and the captured moths counted and removed. During the night, a red safety light was used for the visual examinations. This experiment was replicated twice, once on August 1 (Julian Dt. 213), and once on August 14, 1977 (Julian Dt. 226).

From the data collected by monitoring the flight activity of the population, it was determined that an adult flight could last several weeks. The daily moth catch within each flight was obscured due to the sampling frequency. Therefore, an experiment was conducted in 1978 utilizing similar trapping methods to determine the relationship of trap catch to emergence, oviposition, density, and meteorological conditions. Beginning on July 7, 1978 (Julian Dt. 188), 4 trapping locations containing 1 trap each at a 1.22-m (4') height were baited daily with newly emerged virgin females. Baiting was completed prior to dusk to ensure that each moth was exposed to a normal scotophase. On the following day, the captured male moths were counted and removed, and a new bait was secured within the trap. Generation II was monitored in this manner from July 7 - 26 (Julian Dt. 188-207) and generation III was monitored from August 11 - 28 (Julian Dt. 223-240).

B. Field Ovipositional Studies

On July 26 (Julian Dt. 207) and 27 (Julian Dt. 208), 1977, 3 ovipositional site preference cages, each covering 9 red delicious trees, were erected in random locations in plots 6, 13, and 16. The frame, constructed of 1.91-cm (3/4") conduit and cold rolled steel, measured 1.83 m x 1.83 m x 1.52 m (6' x 6' x 5') and was covered by fiberglass mesh screening. The cage was secured to the ground by guy ropes, and the tails of the screening around the perimeter were buried in the dirt to prevent the escape of the introduced moths. The cages were entered through a snap secured entrance and all the trees were inspected visually. All life stages of A. minuta were removed. Four canopy regions were established within each tree.

Region 1 - main dominant terminal and 20.32 cm (8") down leader

Region 2 - all side terminals and 20.32 cm (8") down branch

Region 3 - area along branches between 20.32 cm - 40.64 cm (8" - 16") from branch terminal

Region 4 - remainder of tree

The relative height and the number of terminals were recorded. On August 1 (Julian Dt. 213), 5 male and 5 female moths that had emerged between July 29 - 31 (Julian Dt. 210-212) were released into each cage. During the following week, the moths were allowed to mate and oviposit. On August 6 (Julian Dt. 218), the cages were entered and eggs oviposited during the week were counted by region and location, top and bottom of leaf. After counting was completed, the cages were removed from the field.

To verify that the data collected in 1977 from the caged ovipositional experiment were indicative of the ovipositional site preferences of the natural population, 2 days were chosen, August 18 (Julian Dt. 230) and September 11, 1978 (Julian Dt. 254), during the 3rd generation moth flight, and egg counts by canopy region were performed on 36 trees each day. Two trees were selected randomly from each variety (Jonathan, yellow delicious, red delicious) within 6 different plots. The height, the number of terminals, the number of eggs in region 1, and the number of eggs in the remainder of the tree were recorded.

C. Developmental Rearing Studies

Three sets of controlled laboratory rearing experiments were conducted in 1979 for the purpose of developing thermal unit models for the various modes of development characteristic of A. minuta. Experiment 1 was a constant temperature rearing experiment utilizing 5 temperatures or treatments, 13°, 15°, 17°, 22°, and 27°C. Each treatment was assigned randomly to a Percival® environmental chamber that had been calibrated within a range of ± 1°C. The humidity within the chambers was maintained by supersaturated salt solutions.

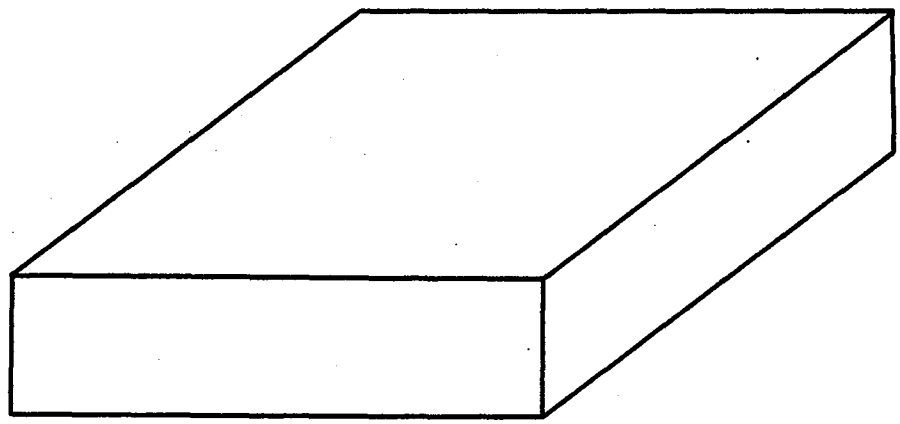
Three hundred sixty eggs oviposited by 10 female moths on a waxed paper substrate during the previous 12 hours were selected randomly as the experimental cohort. Waxed paper disks containing from 1 - 5 eggs each were cut from the ovipositional substrate and were assigned randomly to a treatment temperature. Eggs assigned to each temperature were subdivided randomly into 6 groups. Each of the groups was assigned to one of the

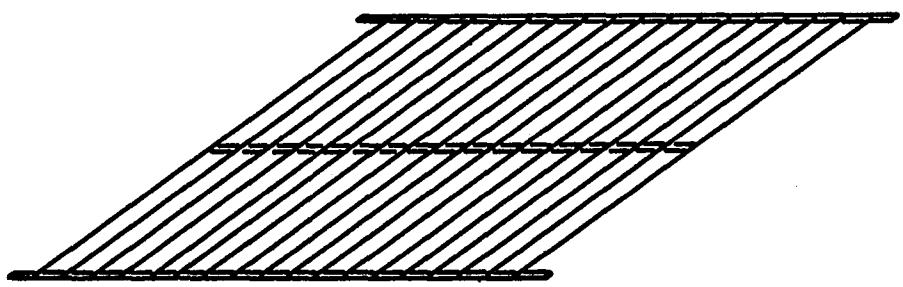
treatment combinations of 3 rearing varieties (Jonathan, red delicious, or yellow delicious) and 2 photoperiods (16 hrs light/8 hrs dark, 12 hrs light/12 hrs dark). A total of 360 insects divided into groups of 12 were reared under 1 of the 30 possible treatment combinations.

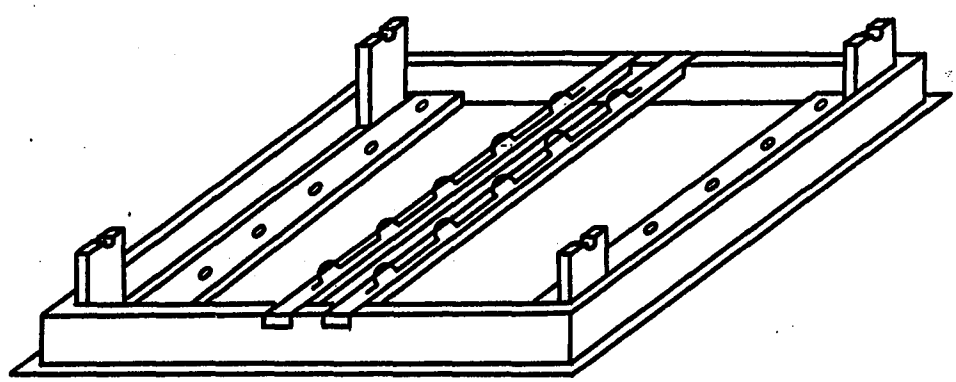
Experiments 2 and 3 were conducted in a similar manner except that the treatment temperatures fluctuated around the mean tempertures, 12°C (T_{max} = 17°, T_{min} = 7°), 15°C (T_{max} = 20°, T_{min} = 10°), 18°C (T_{max} = 24°, T_{min} = 12°), 22°C (T_{max} = 27°, T_{min} = 16°), and 24°C (T_{max} = 31°, T_{min} = 17°). The temperature regimes consisted of 12 hours at the designated high temperature (± 1°C) followed by 12 hours at the designated low temperature (± 1°C). In all of the chambers, the 12 hours of high temperature corresponded to the 12 hours of daylight following the "lights on". For those individuals reared under a 12L/12D photoperiod, the temperature regime and the photoperiod cycled concurrently.

The cohort of eggs designated for each treatment combination was placed in a 29.57-ml (1 oz) clear plastic creamer cup. Three cups of 12 eggs each were positioned on each rearing rack (Figure 5). A chamber contained 2 racks, a 12L/12D rack and a 16L/8D rack. The 16L/8D photoperiod was controlled automatically while the 12L/12D photoperiod was controlled manually. After 12 hours of light, the 12L/12D rack was covered with a "black-out" box (Figure 5) that remained in place for 12 hours until "lights on". Within 1/2 hour after the lights were automatically illuminated for the 16L/8D cohort, the black-out boxes were removed from the 12L/12D rack. Daily at this time, the positions of the racks within each chamber were interchanged to minimize positional effects.

Figure 5. Rearing rack and blackout box used in the developmental rate studies







The eggs were observed daily until eclosion. After eclosion, each 1st instar larva was transferred from the creamer cup to a freshly picked apple leaf. The petiole of the leaf was inserted into a water-filled Aquapic®, and the entire leaf was enclosed in a rearing box (Figure 6). Within each chamber, 36 individuals were reared at each photoperiod, 12 individuals on red delicious, 12 on yellow delicious, and 12 on Jonathan. Every 4 days, each larva was transferred to a fresh leaf picked from single-grafted trees grown in 18.90-l (5 gallon) pots in the insectary greenhouse. All rearing boxes were inspected daily. If a larval molt had occurred, a visual search of the leaf and rearing box was made to locate the shed head capsule. Each recovered head capsule was placed in a gelatin capsule labeled with the temperature, the photoperiod, the specimen number, and the rearing variety. The maximum width of each head capsule was measured and recorded. This procedure was followed throughout the larval stages. By means of a wet/dry bulb thermometer inserted into a rearing box, it was determined that the temperature within the box generally ran 1°C above the ambient chamber temperature and the relative humidity was constantly above 80%.

On the second day post pupation, the pupae were removed from the folded leaves, weighed, sexed, and placed in plastic pockets that had been glued to the side of the rearing boxes (Figure 6). Each box was supplied with an apple leaf to maintain the high relative humidity and to prevent pupal desiccation. The pupae were weighed on a Mettler® balance to the nearest hundredth of a milligram. Two weights were recorded, one from day 2 and one from day 3 post pupation. The sex was determined easily by

counting the number of distinct abdominal segments caudad to the edge of the wing pads (females, 3; males, 4).

Upon emergence, the color morph and the sex were recorded. An attempt was made to pair all newly emergent females with males of the same color morph that had emerged on the same day. Fecundity and ovipositional data from any moths isolated for more than 4 days post emergence were not analyzed. The newly emergent pair was caged in a 5-dram plastic vial with a screen end and a waxed paper liner (Figure 7). A dental wick was inserted into the cap to supply a constant water source. The waxed paper liners were removed daily and the compliment of eggs counted. Each vial was resupplied with water and a new waxed paper liner. Ovipositional vials containing a pair of moths that had been conditioned as larvae to one of the photoperiods were placed on the rearing rack assigned to that photoperiod. This procedure was continued until both moths had died.

A verification experiment was conducted in the insectary greenhouse to determine if the developmental models, constructed from data obtained in controlled laboratory rearings, would describe the development of individuals reared on growing trees under naturally fluctuating temperatures. Six trees, 2 of each variety, were selected randomly from the trees being grown in the greenhouse, and 6 trees, 2 of each variety, were selected from potted trees that had been grown outside. Thus, a total of 12 trees, 4 from each variety, 2 grown inside and 2 grown outside, were utilized as host plants. A hardware cloth cylinder was constructed surrounding each tree. Six terminals were pulled through the holes of the hardware cloth and inserted into funnel rearing cages (Figure 8). One-

Figure 6. Larval rearing box

Figure 7. Adult mating and oviposition cages

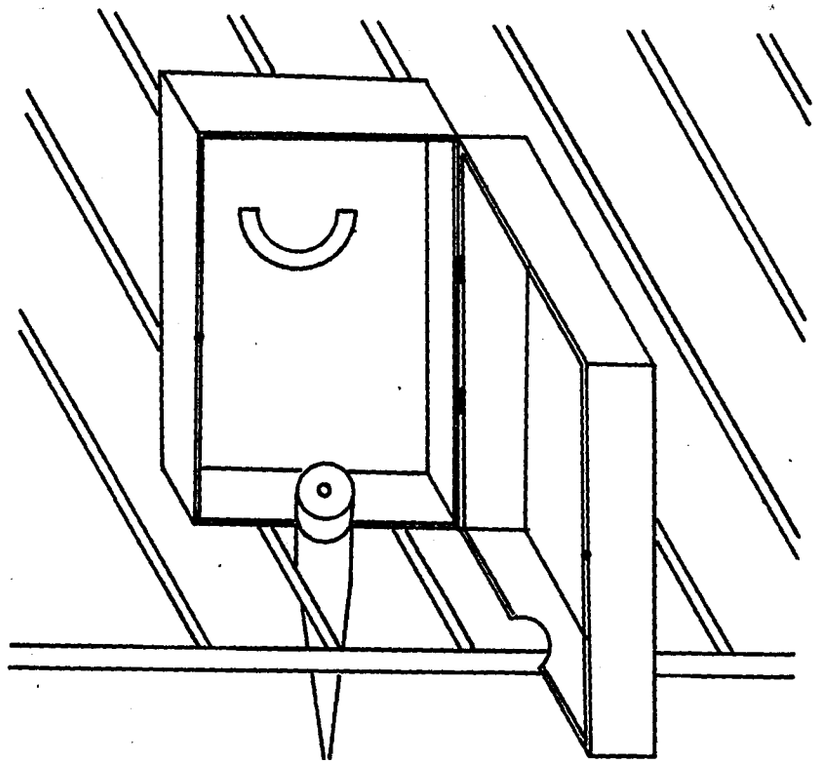


Figure 6.

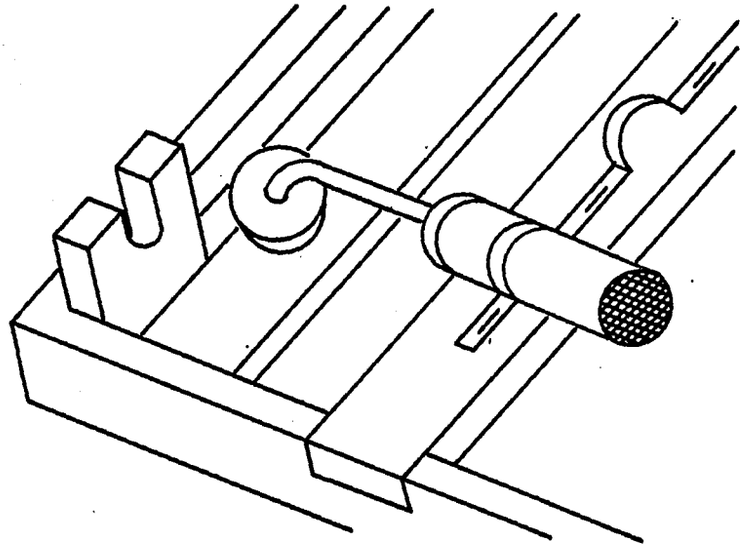
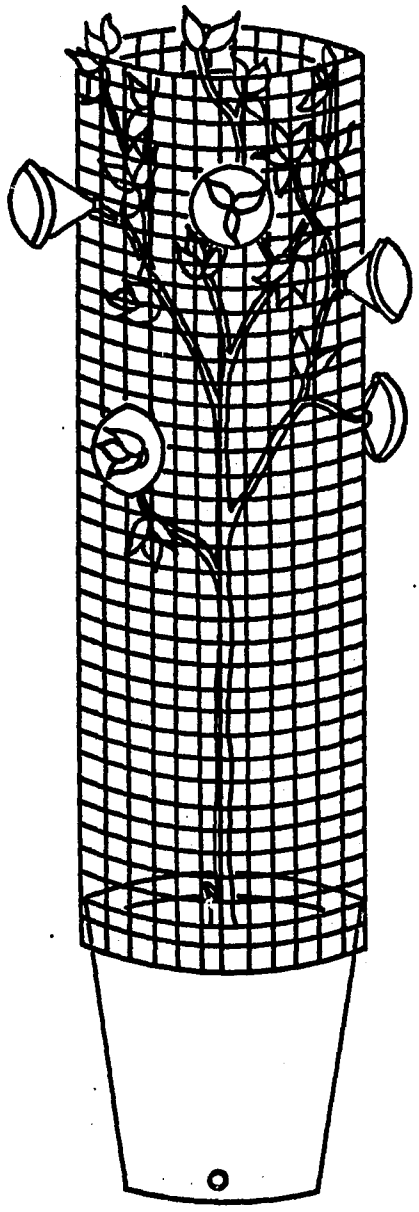


Figure 7.

Figure 8. Larval rearing cages used in the greenhouse verification experiment



half of the cages per tree (3) were randomly designated as 12L/12D cages, and one-half (3) as 16L/8D cages. Eggs selected from several moths were maintained in an environmental chamber under a 16L/8D photoperiod until eclosion. On the day following eclosion, a 1st instar larva was placed into each funnel. Automatic timers controlled the photoperiod (16L/8D) within the greenhouse by illuminating banks of flourescent lamps. After 12 hours of light, all 12L/12D cages were covered with a black vinyl bag that remained in place for 12 hours until "lights on". Within 1/2 hour after the lights were automatically activated, the bags were removed. Development was monitored daily. After a larval molt, the shed head capsule was located and placed in a gelatin capsule. At a later date, the width of all head capsules was measured with an ocular micrometer mounted in a Wild® M5 binocular microscope under 50X magnification.

After pupation, the pupae were removed from the folded leaves and placed in 1-dram vials that had been inserted into the caps of the funnel cages. Pupae were weighed daily on a Mettler® balance to the nearest 0.01 mg. Upon emergence, the sex and the color morph of the adults were recorded.

D. Field Population Studies

During the summer growing season (1976), preliminary information was gathered pertaining to larval and pupal distributions within trees, the number of generations per year, the chronology of moth flights, and the parasitoid complex. Observations of the bionomics of A. minuta established on both dwarf and standard apple varieties were conducted at

2-week intervals. Throughout the summer (1976), specimens were returned to the laboratory to be reared. A synoptic collection of parasitoids was developed and sent to the Insect Identification and Benefical Insect Introduction Institute, Beltsville Agricultural Research Center, Beltsville, Maryland 20705.

More intensive sampling regimes were conducted in 1977 and 1978. In 1977, weekly trips were made to the nursery plots. Population and parasitoid sampling was performed in the field previously described under the adult monitoring section. In order to determine the number of trees per acre available for host habitat, 20 sample sites were selected and the number of viable trees were determined. The destructive sampling procedures used in both the population and parasitoid studies necessitated the development of a scheme that would not re-sample the same trees within any one generation. Beginning at the eastern edge, the first 6 adjacent plots were grouped together into region I followed by plots 7 - 12 in region II, plots 13 - 18 in region III, and plots 19 - 24 in region IV. Plots 25 and 26 were not included in any region. Samples for the parasitoid study were taken in rows 11, 12, 21, & 22 from 1 plot per region on each sampling date. Approximately 100 insects were collected weekly from the trees located in the 4 designated plots. These specimens were returned to the lab for rearing. No tree was re-sampled more often than once every 6 weeks.

Population samples were taken from trees in Jonathan rows 5 - 8, yellow delicious rows 13 - 16, and red delicious rows 26 - 29. One plot per region II and 1 plot per region III were sampled on each date. Ten

trees per variety per plot were selected randomly and searched for life stages of A. minuta. From data gathered in the preliminary studies conducted in 1976, the sampling universe for different life stages was found to vary. In order to sample adequately all the life stages concurrently, the total tree was established as the sampling universe and all A. minuta specimens on designated sample trees were returned to the laboratory. Folded leaves indicative of larval feeding were collected along with leaves containing pupae or eggs. All specimens collected from the 10 sample trees of a single variety and plot were placed collectively in a labeled plastic bag and transported back to the laboratory in a cooler. Due to the sampling procedures, no within tree or between tree comparisons can be made. All larvae and pupae were killed by immersion in KAAD solution and were preserved in 70% ethyl alcohol. The eggs were classified as viable, black head, parasitized or eclosed, and the total numbers recorded. At a later date, the larger larvae were sexed by dissection. Males could be determined by exposing the well-formed testes beneath the dorsal abdominal integument. The width of the head capsules was measured to the nearest 0.02 mm with an ocular micrometer.

The parasitoid samples were reared in individual plastic containers held in an environmental chamber. The rearing containers were constructed from 2, 5 dram plastic vials. The lower vial was the water source for an apple terminal while the upper vial enclosed the leaves and the larva. The larvae were supplied weekly with new terminal shoots picked from mature and declining trees growing within an unmanaged orchard. After pupation, the pupae were enclosed individually with a leaf in a 5-dram

vial. Daily inspections of the vials were made, and parasitoid or adult emergences were recorded. Throughout the summer of 1977, except for a period from May 5 - 27 (Julian Dt. 125-147), procedures described for the parasitoid and population studies were conducted on a weekly basis. Data on generation II are incomplete due to an accidental field insecticide application.

On May 31, 1978 (Julian Dt. 151), a 3rd season of field studies was begun. The same experimental field divided into 26 plots was utilized. Six regions of the field were established. Region I was composed of plots 1 - 4, region II plots 5 - 8, region III plots 9 - 12, region IV plots 13 - 16, region V plots 17 - 20, and region VI plots 21 - 24. Plots 25 and 26 were not included in any region. Eight trees were sampled within each variety from 1 plot per region. A total of 144 trees was sampled every other day from May 31 (Julian Dt. 151), to October 9, 1978 (Julian Dt. 282). A tree that had been selected randomly and sampled was flagged and dated. Trees flagged during the 1st generation were not re-sampled until the 2nd generation moth flight had peaked. Preliminary sampling for 1st generation larvae indicated that the standard error of the mean could be maintained at 15% of the mean infestation level per tree if 130 samples were taken.

Larval and egg samples were taken from the dominant terminal and 20.32 cm (8") down the leader. From data obtained in 1976, it was determined that approximately 40% of the larvae infesting each tree were located in the dominant terminal region. Based on the data obtained from the ovipositional site preference studies conducted in 1977 and 1978, it

was determined that 20% of the eggs found per tree were oviposited in the dominant terminal region. Therefore, the same sampling universe could be established for both life stages. Last instar larvae move down the leader to pupate. A search throughout the canopy of the tree was performed to obtain a pupal sample. All life stages located on the tree within the 2 sampling universes collectively were placed into a plastic bag and transported back to the lab in a cooler. Data collected under this sampling procedure could be analyzed between trees, between varieties, and between plots. No within tree variance can be calculated.

In the laboratory, on the alternate days between sampling dates, each individual within a sample bag was inspected and placed in a 29.57-ml (1 oz) clear plastic creamer cup along with an apple leaf. During the first inspection, the life stage, sex, and condition, i.e., parasitized, not parasitized, viable, not viable, were recorded. Larval head capsule measurements were recorded in order to determine the instars. Two days later, a subsequent inspection of each sample was performed to determine the condition of the individual. Fifty percent of the samples were selected randomly and retained to be used in the parasitoid and mortality studies. The remainder of the samples were discarded. During the second inspection and every 4 days, the retained larvae were provided with new leaves. Those individuals held within the laboratory for the parasitoid study were inspected daily, and emergences and mortality were recorded.

IV. RESULTS AND DISCUSSION

A. Adult Flights

1. Seasonal adult flights

Acleris minuta is a multivoltine species with 4 generations in southwestern Iowa. The first adult flight occurs when the overwintering (gray) moths break diapause in the spring. The next 3 adult flights are composed predominantly of summer (orange) moths while the 5th adult flight is composed predominantly of winter (gray) moths. During the summer of 1977, virgin female baited trap catches indicated that live females could attract males in numbers large enough to determine peak trapping periods. Baited traps caught more males than did unbaited traps at both the 0.30-m and the 1.22-m heights. Because no significant differences occurred between baited treatments at the 0.30-m and the 1.22-m heights or between unbaited treatments at the 0.30-m and the 1.22-m heights, treatment heights were combined. Analysis of variance performed separately on 27 weekly trapping periods indicated that the mean number of summer (orange) males caught in baited traps was significantly different ($p < .01$) from the mean number caught in unbaited traps. The data for all virgin female baited trapping periods were summarized (Table 2). The success of this trapping method is because of the appetitive searching behavior demonstrated by summer males in response to the pheromone calling bouts performed by the summer female. Traps were baited with virgin females 20 of the 29 weeks between April 7 (Julian Dt. 97) and October 29 (Julian Dt. 301). A total of 18,592 moths were caught throughout the summer and weekly trap catches ranged from 0 - 411 moths.

Table 2. Mean number of males caught in virgin female baited traps (1977)

T.U.s[a]	Julian Dt.	Visit No.	N[b]	Trap catch (Summer)		Trap catch (Winter)	
				$\bar{x}$	S.E.	$\bar{x}$	S.E.
0.00	97	1	*			WINTER MOTH FLIGHT	
64.95	104	2	*				
130.21	111	3	*				
185.70	118	4	*				
255.68	125	5	*				
340.71	134	6	12	55.75	7.64		
517.05	147	7	9	56.78	11.37		
592.00	153	8	+	35.50			
705.06	160	9	*				
815.61	167	10	*				
931.19	175	11	11	96.91	8.50		
1034.81	182	12	22	95.59	7.79		
1150.88	188	13	24	59.71	12.19		
1284.24	196	14	24	37.50	6.32		
1417.85	203	15	*				
1525.90	210	16	16	34.69	8.61		
1652.88	218	17	24	213.00	16.74		
1734.22	224	18	21	42.52	6.97		
1810.55	230	19	24	49.79	8.90		
1930.35	239	20	21	45.95	5.20		
1993.05	244	21	15	20.00	5.42		
2096.99	252	22	12	35.58	8.39		
2163.36	259	23	14	22.29	5.57		
2241.11	266	24	16	13.69	3.21	0.44	0.20
2306.67	273	25	23	9.96	1.57	2.52	0.54
2337.71	280	26	24	0.04	0.04	0.29	0.11
2365.08	287	27	24	0.17	0.10	0.42	0.19
2407.74	294	28	12			4.08	2.10
2442.97	301	29	12			7.42	2.02

[a] T.U.s = (Tmax + Tmin/2) - 8.85°C, if Tmin < 8.85°C then Tmin = 8.85°C.

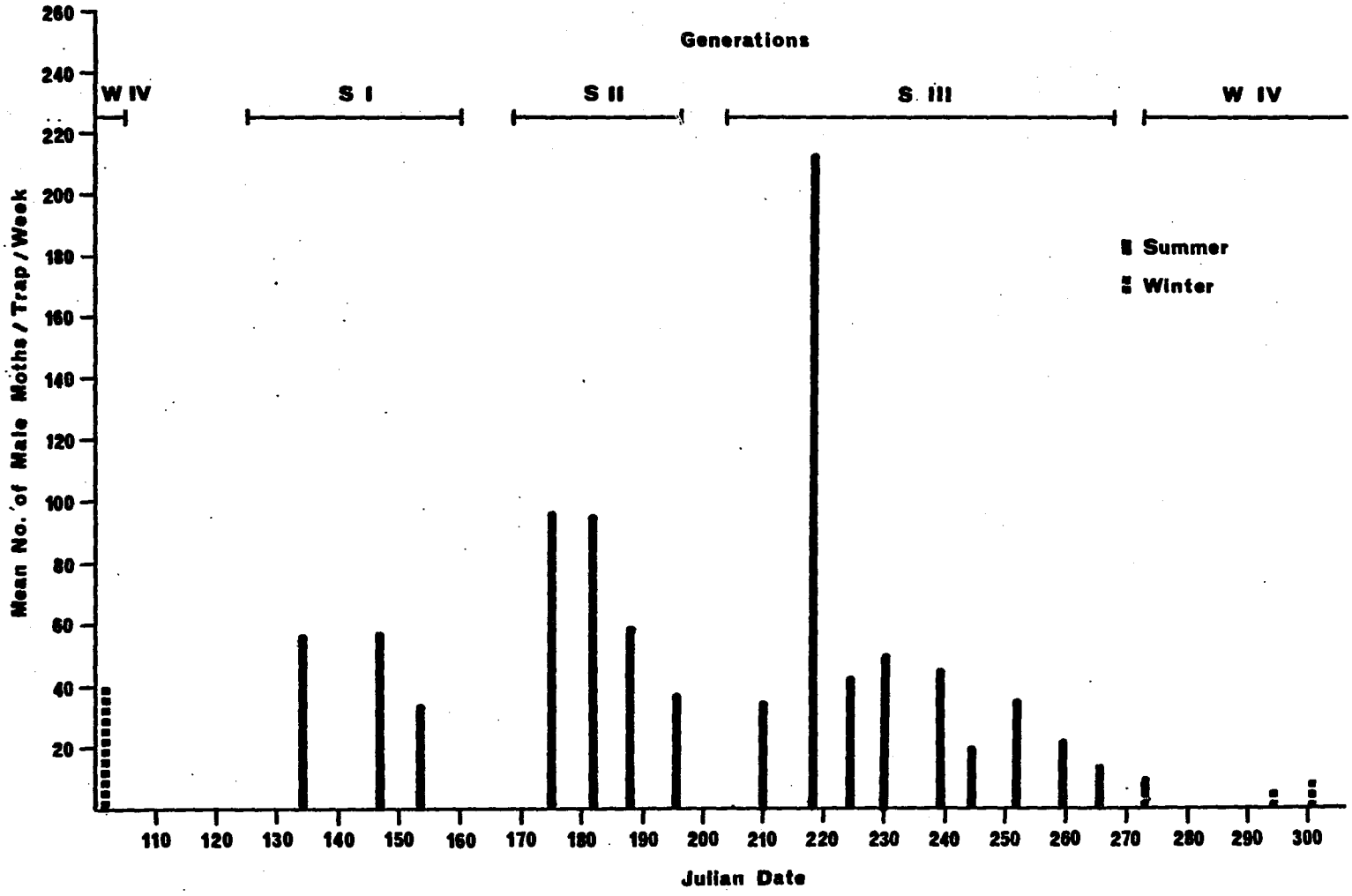
[b] * = traps not baited with virgin females; + = virgin female baits died during trapping period.

Winter (gray) moths that had emerged in the fall of 1976 and overwintered were sighted on April 7 (Julian Dt. 97) flying and ovipositing eggs on the bark of grafted apple nursery stock. Oviposition of fertile eggs by the winter (gray) females indicated that mating of at least a proportion of the population had occurred by this date. On April 14 (Julian Dt. 104), winter moths were not active during the normal ovipositional time period (1800 - 2100 CDST) and no additional winter moths were sighted after this date.

Summer (orange) females were available to use as bait during the period from May 14 (Julian Dt. 134) to June 2 (Julian Dt. 153) and orange males were caught in sufficient numbers to indicate the presence of the first summer flight (SI) (Figure 9). The traps were not baited again until June 24 (Julian Dt. 175) when a mean of 96.91 moths per trap was caught during the weekly trapping interval. The second summer flight (SII) occurred during this time, but it was impossible to tell whether the sample taken on June 24 (Julian Dt. 175) represented the peak catch (Figure 9). The third summer flight (SIII) peaked on August 6 (Julian Dt. 218) with a mean of 213 moths per trap (Figure 9). Those individuals captured after September 16 (Julian Dt. 259) probably were aberrant orange color morphs of the normally gray fourth adult generation (WIV) (Figure 9).

Winter moths, that were never trapped prior to September 16 (Julian Dt. 259), were trapped in very limited numbers after this date (Figure 9). Because baited traps were slightly more efficient at capturing winter males than unbaited traps, gray males apparently respond to calling orange females. Emergence of the gray generation occurred between September 16

Figure 9. Frequency histogram of the mean number of males trapped per week (1977)


Generations
W IV
S I
S II
S III
W IV
Summer
Winter
Mean No. of Male Moths / Trap / Week
260
240
220
200
180
160
140
120
100
80
60
40
20
110
120
130
140
150
160
170
180
190
200
210
220
230
240
250
260
270
280
290
300
Julian Date

(Julian Dt. 259) and October 29 (Julian Dt. 301); however, the mean trap catch did not reflect the increasing population density of newly emerging gray males. While gray males may be capable of responding to pheromones, the efficiency of the pheromone communication system as evidenced by trap catches is much less than the efficiency associated with summer generations.

While mean weekly trapping intervals were frequent enough to delineate adult flights, temporal relationships between trap catch and population phenology were obscured by infrequent sampling. Therefore, in 1978, daily trap catches were monitored during the SII generation, July 7 (Julian Dt. 188) to July 28 (Julian Dt. 207), and during the SIII generation, August 12 (Julian Dt. 224) to August 28 (Julian Dt. 240).

Throughout the trapping periods, trap catch variance was high with the daily standard error of the mean averaging approximately 34% of the mean trap catch. By monitoring additional traps, it may have been possible to reduce the variance making the daily mean trap catch more indicative of the population behavior and phenology. Frequency histograms display the mean daily male trap catch for the SII and SIII generations (Figures 10. A, 11. A) compared with the temperature (°C), the wind velocity (kph), and the relative humidity (%) as measured during the calling period (0600 CDST) for each sampling date (Figures 10. B, C, D; 11. B, C, D). Fluctuations in mean daily trap cach probably result from 1) changes in adult populations due to changes in population phenology, 2) modifications in male searching behavior brought about by exogenous environmental factors, and 3) variations in female attractancy associated

Figure 10. Virgin female baited trap catches and environmental conditions during the SII generation (1978): (A.) Frequency histogram of the mean number of male moths trapped per night; (B.) daily temperature (°C) measured at 0600 CDST; (C.) daily wind velocity (kph) measured at 0600 CDST; (D.) daily relative humidity (%) measured at 0600 CDST

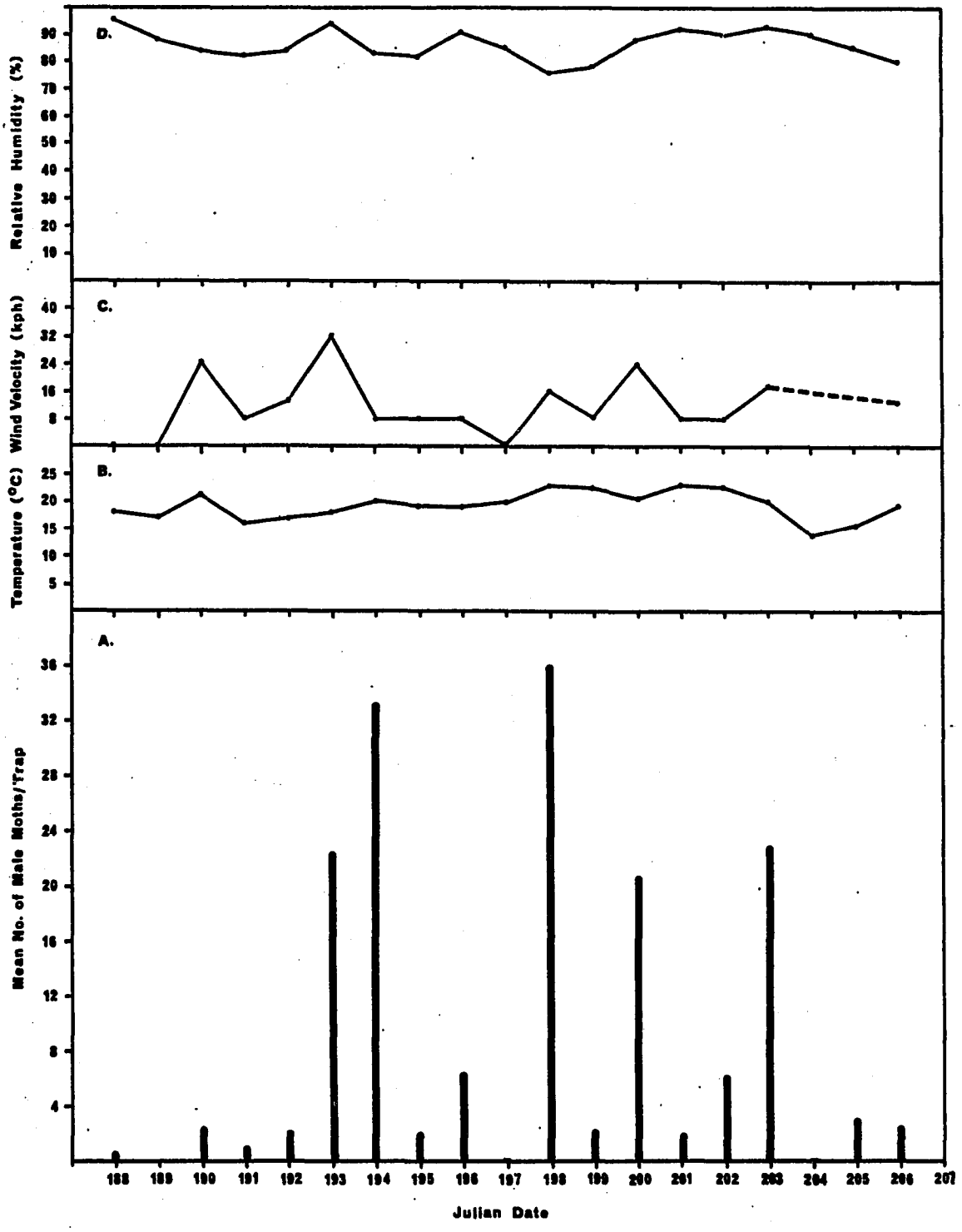
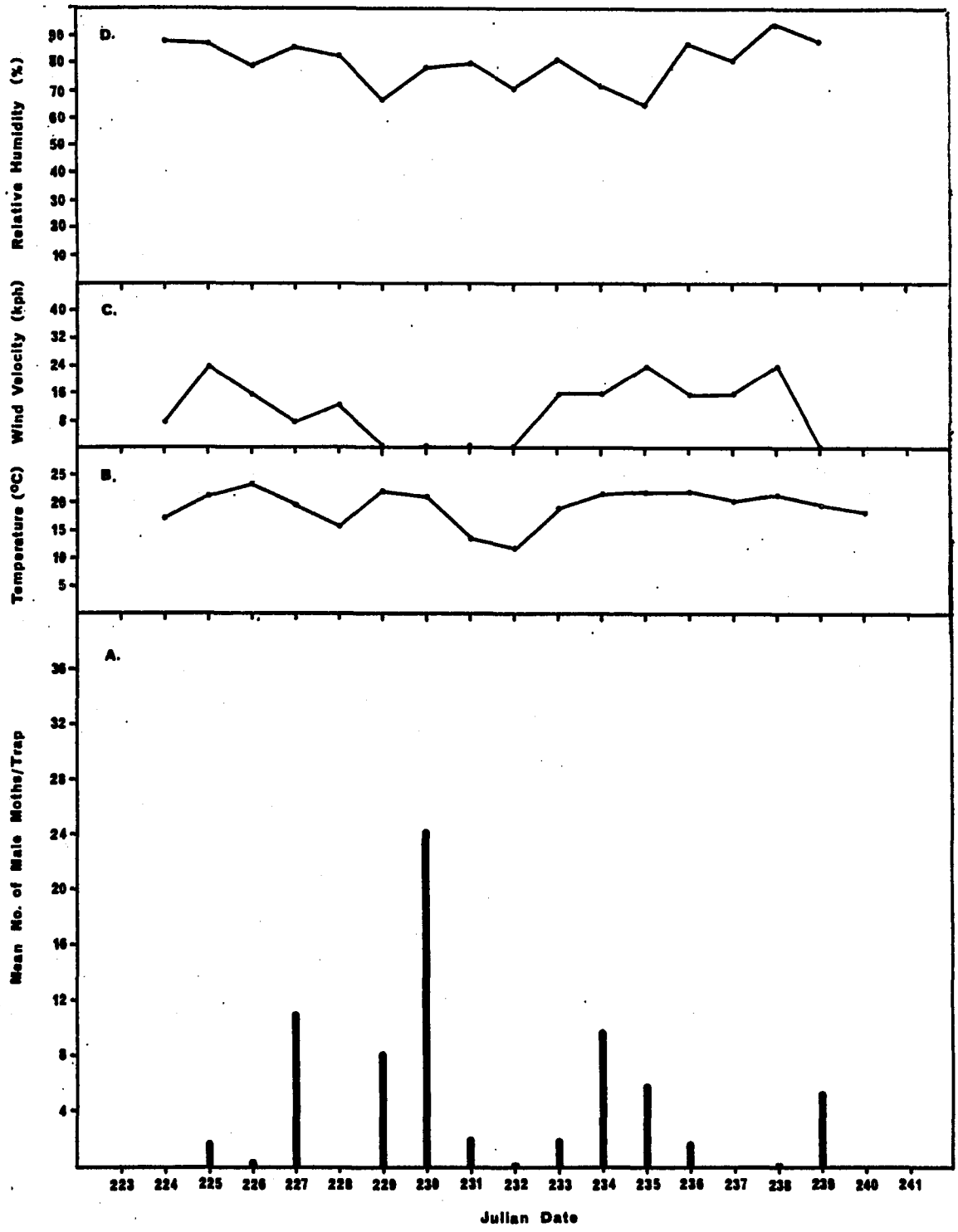

D.
Relative Humidity (%)
C.
Wind Velocity (kph)
B.
Temperature (°C)
A.
Mean No. of Male Moths/Trap
Julian Date

Figure 11. Virgin female baited trap catches and environmental conditions during the SIII generation (1978): (A.) Frequency histogram of the mean number of male moths trapped per night; (B.) daily temperature (°C) measured at 0600 CDST; (C.) daily wind velocity (kph) measured at 0600 CDST; (D.) daily relative humidity (%) measured at 0600 CDST


D.
Relative Humidity (%)
C.
Wind Velocity (kph)
B.
Temperature (°C)
A.
Mean No. of Male Moths/Trap
Julian Date
223 224 225 226 227 228 229 230 231 232 233 234 235 236 237 238 239 240 241

with the population under varying environmental conditions. A high majority (88%) of the days with trap catch peaks (daily trap catch > 10 males) occurred on days when the temperature during the calling period (0600 CDST) was $\geq$ 20°C. However, only 44% (gen. SII) and 27% (gen. SIII) of the days with temperatures $\geq$ 20°C had peak trap catches. Additional error may have been introduced into the third generation trap catches during the period from Aug. 19 (Julian Dt. 231) to Aug. 28, 1978 (Julian Dt. 240). Because procedural error during this period resulted in an extended photophase, virgin females used as bait may have been entrained to an atypical photoperiod. Independently, temperature fluctuations cannot explain trap catch frequencies. In all cases during this study, temperatures below 15°C were associated with low daily trap catches. Wind velocity within the 8-32 kph range did not affect trapping efficiency noticeably. However, the wind velocity within the canopy, the area where oriented moth flight occurs, was not monitored. The canopy wind velocity would be considerably less than the velocity recorded. Some air movement would facilitate the dispersal of the pheromone plume and probably would be beneficial. However, wind velocities that interfere with the upwind flight of the males would prevent them from reaching pheromone sources, decreasing the efficiency of pheromone trapping.

2. Daily mating flights

During the third summer moth flight, an hourly trapping scheme was replicated on August 1 (Julian Dt. 213) and on August 14, 1977 (Julian Dt. 226). Summer adults were active from 0500 to 0800 CDST. Peak

attractancy on both days occurred at false dawn between 0500 and 0600 CDST, a period of increasing illumination that occurred approximately 30 minutes before actual sunrise. Four times more males were captured during this hour than at any other hour during the activity period (Table 3). A 98% decrease in trap catch was observed during the hourly interval (0600 - 0700 CDST) following the peak activity period. Whether this dramatic drop in trap catch results from the termination of pheromone emission, the saturation of the air space within the habitat, or the habituation of the male neural receptor system has not been determined. Each of these processes requires a recycling period that readies the population for successful precopulatory behavior and mating during the daily circadian gate (0500 - 0800 CDST).

3. Temporal relationships between adult flights and population phenology

The temporal relationship between trap catch and field emergence of male moths should indicate the sensitivity of this virgin female baited trapping technique. Field emergence was not monitored. However, laboratory emergence data suggest that protandry is characteristic of the species. Under fluctuating temperatures, male moths emerge approximately 15 thermal units (T.U.s) prior to female moths. This 15 T.U. difference would result in males emerging 1 day earlier than females during typical July and August T.U. accumulations. Biofix 1 (first significant uninterrupted trap catch) should occur 1 day prior to significant female emergence. Field emerging females mate and begin ovipositing during day 1 post emergence. Because field emergence of males and/or females was not

Table 3. Mean number of males caught during hourly intervals in virgin female baited traps (1977)

CDST	Julian Dt. 213 $\bar{x}$	Julian Dt. 226 $\bar{x}$
0100	0	0
0200	0	0
0300	0	0
0400	0.17	0.13
0500	9.88	2.04
0600	34.63	4.29
0700	0.79	0.04
0800	0.21	-
0900	0.08	-
1000	0	-

monitored directly, the relationships between trap catch and pupation, and trap catch and oviposition were investigated. If virgin female baited traps are attractive to field males, the first significant trap catch should occur just prior to the beginning of the ovipositional period. Biofix 1 for the SII generation occurred on July 9 (Julian Dt. 190); this corresponded to the date when 33% of the sampled population had pupated and 1% of the eggs (generation SIII) had been oviposited (Table 4). Biofix 1 for the SIII generation occurred on August 13 (Julian Dt. 225); this corresponded to the date when 64% of the sampled population had pupated and 4% of the eggs (generation WIV) had been oviposited (Table 5). The cumulative percentage trap catch was calculated by 1) summing all daily mean trap catches for each flight (SII, SIII), 2) expressing the daily mean trap catch as a percentage of the total generation catch, and 3) accumulating the daily percentages throughout the flight. The cumulative percentage pupation and the cumulative percentage oviposition were calculated for the SII and SIII generations from data obtained during field population studies. The cumulative percentage pupation was calculated by 1) summing the daily pupal densities for each generation, 2) expressing the daily pupal density as a percentage of the summated pupal densities, and 3) accumulating the daily percentages beginning on the date pupae were first discovered in the field. Similarly, the cumulative percentage oviposition for each generation was calculated by 1) expressing daily egg densities as a percentage of the summated egg densities, and 2) accumulating the percentages for the SII and the SIII ovipositional periods. During both generations, Biofix 1 coincided with

Table 4. Cumulative percentage trap catch, cumulative percentage pupation, and cumulative percentage oviposition for the SII generation (1978)

T.U.s[a]	Julian Dt.	Cum. % Catch [b]	Cum. % Pup.[b]	Cum % Ovip.[b]
836.08	183		6	
854.73	184			
874.77	185		10	
896.20	186			
914.29	187			
927.66	188		20	
940.75	189			
954.40	190	2	33	1
964.99	191	2		
975.86	192	4	55	2
992.57	193	18		
1006.78	194	37	72	3
1020.15	195	38		
1036.30	196	42	84	12
1053.56	197	42		
1072.77	198	64	91	23
1091.14	199	65		
1108.40	200	78	98	47
1124.83	201	79		
1139.59	202	83		
1152.96	203	96	99	65
1164.39	204	97		
1176.93	205	98	99	79
1193.91	206	100		
1210.34	207		100	85
1224.55	208			
1241.81	209			95
1256.57	210			
1270.22	211			97
1283.87	212			
1298.35	213			98
1312.28	214			
1322.60	215			99
1330.97	216			
1341.84	217			99
1355.77	218			
1371.64	219			100

[a] T.U.s = (Tmax + Tmin/2) - 8.85°C, if Tmin < 8.85°C then Tmin = 8.85°C.

[b] See section IV. A. 3 for definition of cum. % catch, cum. % pupation and cum. % oviposition.

Table 5. Cumulative percentage trap catch, cumulative percentage pupation, and cumulative percentage oviposition for the SIII generation (1978)

T.U.s[a]	Julian Dt.	Cum. % Catch[b]	Cum. % Pup.[b]	Cum. % Ovip.[b]
1432.64	223		43	
1448.23	224			
1467.44	225	2	64	4
1487.76	226	3		
1505.30	227	18	83	13
1520.34	228	18		
1539.82	229	29	90	26
1557.64	230	62		
1569.62	231	65	94	33
1579.64	232	65		
1597.18	233	68	97	35
1616.39	234	82		
1636.43	235	90	99	43
1653.69	236	92		
1672.62	237	92	100	44
1690.16	238	92		
1707.14	239	99		46
1721.90	240			
1732.77	241			57
1743.64	242			
1755.62	243			78
1771.49	244			
1787.64	245			88
1804.35	246			
1821.33	247			93
1838.31	248			
1856.96	249			96
1876.44	250			
1893.98	251			
1909.57	252			96
1925.72	253			
1942.43	254			
1959.97	255			97
1975.01	256			
1986.16	257			97
2000.64	258			
2017.07	259			97
2029.33	260			
2045.76	261			98

[a] T.U.s = (Tmax + Tmin/2) - 8.85°C, if Tmin < 8.85°C then Tmin = 8.85°C.

[b] See section IV. A. 3 for definition of cum. % catch, cum. % pupation and cum. % oviposition.

the beginning of the ovipositional period. SII and SIII female baited traps continued to capture males for 239 T.U.s, indicating that the adult flights for both generations were of similar duration. Chronologically, the SII flight lasted 2 days longer than the SIII flight; however, this would be expected if the increased daily T.U. accumulation during the SIII generation accelerated larval development and oviposition, truncating the adult flight.

The biofix concept appears to establish a reliable starting point for summer (orange) generations. Rate functions, e.g., ovipositional rate, developmental rate, etc., driven by T.U. accumulations can be synchronized based upon this starting point. Biofix 1 coincides well with the beginning of the adult ovipositional period. Therefore, the population development for a generation could be predicted to begin on a particular date based upon a physiological response of the preceding adult population.

While the biofix concept appears to establish a reliable starting point for the SII, SIII, and WIV generations, the use of the biofix concept to establish the beginning of the SI generation requires further investigation. SI eggs are oviposited in the spring by gray females who have overwintered successfully and mated. Laboratory experiments indicate that, unlike newly emerged orange moths, newly emerged gray moths are not capable of mating. Dissections of the reproductive systems of both newly emerged orange and gray moths reveal no morphological differences. However, the precopulatory and copulatory behaviors that facilitate mate location and copulation are not performed by newly emerged gray moths.

Based upon these observations, mating of the overwintering generation probably does not occur upon emergence in the fall, but rather occurs in the spring by those individuals who have broken diapause and developed the ability to perform the necessary precopulatory and copulatory behaviors. Assuming that the gray color morph utilizes the same pheromone communication system, the ability to perform precopulatory behaviors, e.g., mate location, is a prerequisite to successful pheromone trapping. Therefore, the theoretical biofix for the WIV generation should occur when environmental conditions promote the termination of diapause and the development of the pheromone communication system. The conditions that lead to the termination of diapause are not known. Adaptive pressure probably ensures that diapause is terminated when mating period temperatures, ovipositional period temperatures and daily developmental temperatures equal or exceed the threshold temperatures (7 - 10°C). Shortened photophases (< 14 hours) cause larvae to develop into gray moths. It is likely that increasing photophases play an important role in diapause termination. The theoretical biofix, the first significant uninterrupted trap catch, should occur when photophases increase to approximately 13 hours and temperatures at 0600 CDST average more than 8.85°C.

B. Reproductive Rate

The net reproductive rate for any generation of a designated A. minuta population is dependent upon the reproductive potential and the reproductive efficiency of the population during a specified time inter-

val. The reproductive potential of a population is the maximum number of eggs the population is capable of producing while the reproductive efficiency of the population is the proportion of the reproductive potential that is oviposited. Dynamic qualities that help define the net reproductive rate for a generation include: 1) the mating efficiency, 2) the fecundity of the generation, 3) the ovipositional pattern, and 4) the longevity of the reproductively active females. Any one of these qualities may vary and there is some indication that the variations are direct results of the conditions existing during the specified generation. If average conditions can be defined for each generation, the net reproductive rate will be predicted more accurately, reflecting seasonal changes in climate and in nutritional values of host plants.

1. Mating behavior and mating efficiency

The environmental conditions that mediate mating can be divided into those that trigger or stimulate mating and those that promote or do not hinder associated mating behaviors. The importance of photoperiod as an entraining stimulus setting the circadian gate for precopulatory behavior has been documented well for lepidopterous insects. Photoperiod may be the only environmental stimulus that is seasonal and absolute based upon a chronological scale. Both laboratory and field observations of orange moths support the entraining hypothesis requiring a "lights-on" stimulus to induce calling.

Assuming that development has proceeded through the orange color morph scheme, calling and mating should occur 1 day post emergence during

the entrained activity period. The temperature during this activity period must equal or exceed the mating threshold temperature.

Laboratory mating success rates were determined under fluctuating temperature regimes designated by the mean temperatures of 12°, 15°, 18°, 22°, and 24°C. Actual temperatures during the mating period were 7°, 10°, 12°, 16°, and 17°C. A female ovipositing fertile eggs was considered to have mated successfully. Mating was assumed to occur on the first day that fertile eggs were oviposited. Under optimal conditions, this assumption is correct. Under adverse conditions, the temporal relationship between mating and oviposition may vary. Mating success rates averaged 14% at 12°C, 73% at 15°C, 90% at 18°C, 77% at 22°C, and 83% at 24°C. At mating period temperatures > 10°C, approximately 83% of the females mated and oviposited fertile eggs. Under these conditions, 83% of these females mated and oviposited on day 1 post emergence. An additional 6% of these females mated and oviposited on day 3 post emergence, and an additional 11% mated and oviposited on day 4 post emergence. However, when the mating period temperature was > 7°C but ≤ 10°C approximately 73% of the females mated and oviposited fertile eggs. The daily mating and ovipositional success rates of these females on days 1, 2, 3, and 4, post emergence, averaged 18, 55, 18 and 10%, respectively. At 7°C, the mating success rate decreased to 14%. This drastic decrease in mating success from 73% (15°C) to 14% (12°C) indicates that the mating threshold temperature is between 7° and 10°C.

Field mating period mean temperatures during all the summer flights exceeded the mating threshold temperature. Under field conditions (1978)

the temperature at 0600 CDST (false dawn) averaged 16.57°C for the SI adult flight, 19.42°C for the SII flight, and 19.83°C for the SIII flight (Table 6). The unusually long emergence period for the WIV generation (approximately 41 days) resulted in a mean mating period temperature (9.73°C) close to the mating threshold. During the first half of the WIV emergence period (Julian Dt. 258 - 278), when approximately 80% of the fall emergence occurred, mating period temperatures averaged 12.86°C, well above the mating threshold. Therefore, it can be assumed that temperature would not hinder mating if the gray population were physiologically or behaviorally capable of mating. The mating period temperatures during the spring WIV flight (Julian Dt. 91 - 97) averaged 8.83°C. This mean mating period temperature closely approximates the mating threshold.

Laboratory conditions that normally produce an 81% mating success rate for orange moths will not induce mating of newly emerged gray females with either orange or gray males. Newly emerged gray moths will not mate when held under a 12L/12D photoperiod (simulated fall photoperiod) or a 16L/8D photoperiod (simulated summer photoperiod). Gray moths, both males and females, are responsive to "lights-on", the environmental stimulus that induces orange moth mating. After a 12 hour scotophase, gray moths will extend their antennae from the concealed "resting" position with the introduction of light. However, the appetitive searching behavior typical of orange males caged with orange females does not occur. Neither orange males nor gray males demonstrate the stereotyped wing fluttering when caged with gray females. This wing fluttering precopulatory behavior has been observed only in response to females who have assumed the calling

Table 6. Environmental conditions monitored during the mating activity period of the adult flights (1978)

Environmental Condition	SI	SII	SIII	WIV (fall)
°C (0600 CDST)				
$\bar{x}$	16.57	19.42	19.83	9.73
S.D.	3.45	2.72	3.20	5.54
Wind Velocity				
$\bar{x}$ (kph)	10.46	10.14	10.86	10.14
S.D.	12.89	8.93	9.61	10.59
Barometric Pressure				
$\bar{x}$ (cm)	75.79	75.77	75.64	76.25
S.D.	0.36	0.28	0.38	0.58
Relative Humidity				
$\bar{x}$ (%)	72.33	85.65	80.20	78.76
S.D.	10.45	6.65	8.21	10.05

posture or to abdominal washes of calling orange females. Because newly emerged gray females have not been observed in the calling position, it appears that these gray females are not physiologically capable of calling. Newly emerged orange moths will mate when held under simulated summer and fall photoperiods. If orange moths were produced during the fall generation, mating induced by photoperiod potentially would be successful. The fact that orange moths will mate during fall photoperiods while gray moths will not indicates that a difference in physiological readiness must exist between the 2 color morphs.

While orange moths do not diapause, gray moths do diapause (overwinter) and diapause may be obligatory. Only by diapausing can gray moths survive the winter and thus experience the environmental conditions of spring and summer that promote the physiological development of pheromone production and calling behavior. Based upon this hypothesis, mating of gray females does not occur until spring, requiring the successful overwintering of both males and females. The physiological capacity of newly emerged gray males to inseminate receptive females has not been investigated. It is likely that the gray male's physiological maturation closely parallels the delayed female maturation, thus synchronizing spring mating.

Mating efficiency can be defined as the number of successful matings that result in oviposition of fertile eggs divided by the number of potentially eligible mating pairs. Summer generations with a 1:1 sex ratio (males:females) and with males capable of inseminating more than 1

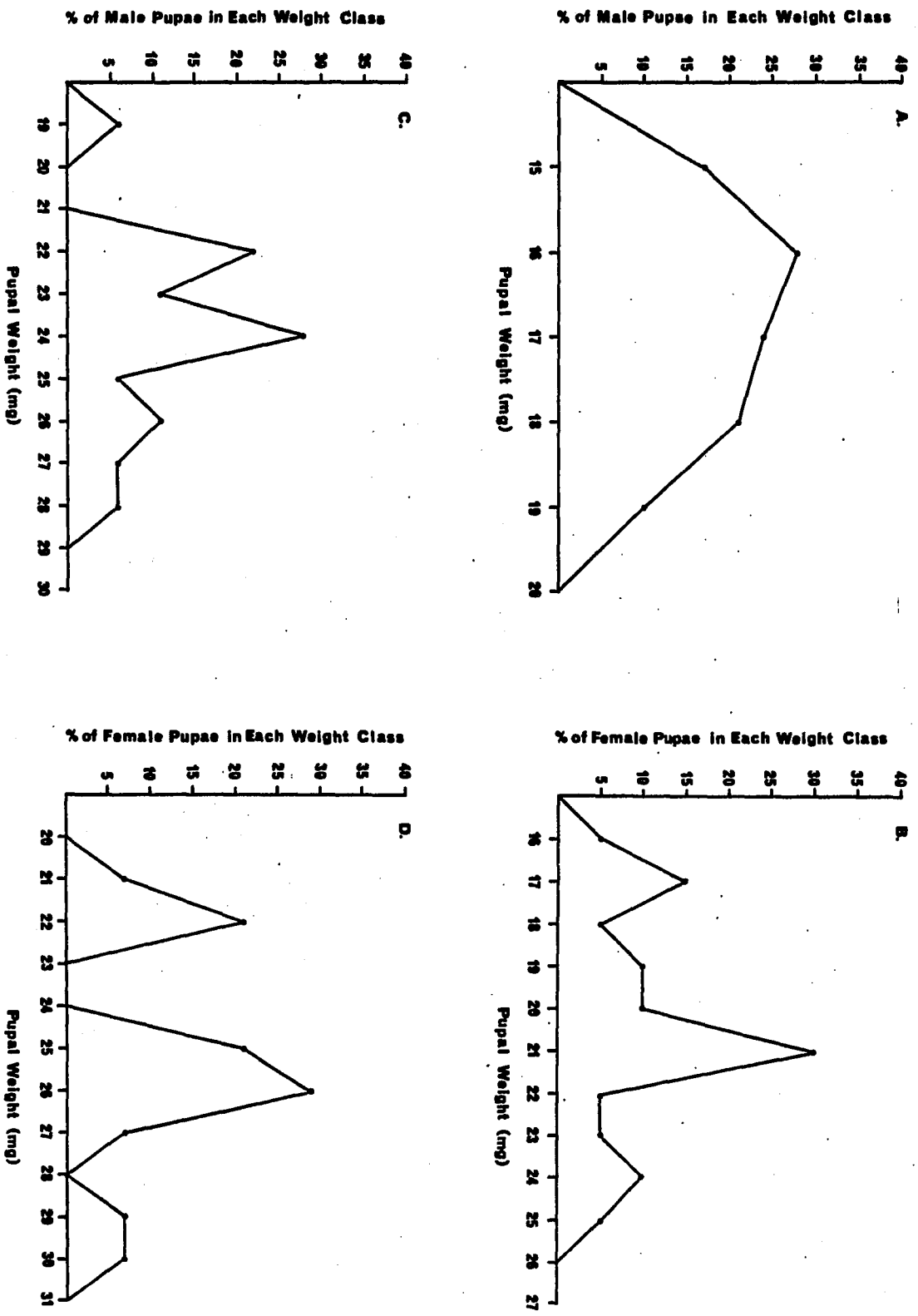
female have a surplus of male mates. Therefore, the mating efficiency can be defined as the proportion of females, given the opportunity to mate, that oviposit fertile eggs. Successful matings are dependent upon: 1) the female's competitive ability to attract fertile males, and 2) the physiological fitness of both males and females. Field mating efficiencies for summer generations have not been determined.

The sex ratio of the emerging WIV generation deviates from the 1:1 ratio (males:females) associated with summer generations. In 1977 and 1978, the sex ratio was 2.33:1.00 and 1.63:1.00, respectively. This imbalance in favor of males increases the probability of successful mating. Males may or may not experience greater overwintering mortality, but the 2:1 sex ratio typical of WIV generations insures that adequate males are available in the spring to inseminate surviving females.

2. Fecundity

During the summers of 1976 and 1977, field observations indicated that female size varied in a systematic relationship to generation. Pupal weights were measured as an index of adult size and potential fecundity. Pupal weights for 83 field individuals were measured from collections made during the SII and WIV generations (1977). More SII female pupae (30%) belong to the 21-mg weight class than to any other weight class (Figure 12. B). More SII male pupae (27%) belong to the 16-mg weight class (Figure 12. A). The modes of the pupal weight class distributions for WIV females and WIV males are 26 mg and 24 mg, respectively (Figures 12. C, D). A significant difference ($P < .01$) exists between the mean pupal

Figure 12. Weight class distributions of male and female pupae of the summer and winter color morphs (1977): (A.) Percentage of the SII male pupae in each weight class; (B.) percentage of the SII female pupae in each weight class; (C.) percentage of the WIV male pupae in each weight class; (D.) percentage of the WIV female pupae in each weight class


% of Male Pupae in Each Weight Class
A.
Pupal Weight (mg)
% of Male Pupae in Each Weight Class
C.
Pupal Weight (mg)
% of Female Pupae in Each Weight Class
B.
Pupal Weight (mg)
% of Female Pupae in Each Weight Class
D.
Pupal Weight (mg)

weights of the summer (18.0 mg) and winter (24.2 mg) color morphs with the mean weight of a winter pupa being approximately 6 mg heavier than a summer pupa. Statistical comparisons between male and female mean pupal weights did not indicate a significant difference at the .05 level of significance; however, an apparent trend exists for females to weigh approximately 2 mg more than males. Within the SII and the WIV generations, no significant differences exist among pupal weights of males reared on Jonathan, yellow delicious, or red delicious cultivars or among pupal weights of females reared on Jonathan, yellow delicious, or red delicious cultivars (Table 7).

Generally, pupae of the summer generations appear to decline in size and consequently weight with the largest pupae developing during the SI generation, followed by SII pupae, that appear to be larger than SIII pupae. The winter generation, WIV, while developing more slowly than the summer generations reach a significantly larger pupal size. Because oviposition by the winter generation occurs the following spring, this larger size probably is of adaptive significance to the overwintering adult moth.

In order to develop a relationship between pupal weight and realized laboratory fecundity, pupae reared during the developmental rate experiments were used. Females and males reared at 12°, 15°, 18°, 22°, and 24°C mean fluctuating temperatures were caged in pairs and allowed to mate. Daily ovipositional cohorts were counted and summated for each pair until the female died. Females that did not oviposit by the second day post emergence or did not oviposit fertile eggs were not included in the

Table 7. Mean pupal weight (mg) of field collected pupae (1977) grouped by generation; generation and sex; and generation, sex, and variety

Generation[a]	Sex[b]	Variety[c]	N	Mean weight ± S.D.[d]	
SII			50	18.0 ± 2.8	a
WIV			33	24.2 ± 2.8	b
SII	M		29	16.7 ± 1.3	a
SII	F		21	19.7 ± 3.2	a
WIV	M		18	23.4 ± 2.9	b
WIV	F		15	25.2 ± 2.5	b
SII	M	JON	10	17.4 ± 1.0	a
SII	M	YDEL	11	16.4 ± 1.6	a
SII	M	RDEL	8	16.2 ± 0.9	a
SII	F	JON	7	21.7 ± 1.4	a
SII	F	YDEL	5	18.9 ± 1.8	a
SII	F	RDEL	9	18.4 ± 4.2	a
WIV	M	JON	7	24.5 ± 2.0	b
WIV	M	YDEL	8	22.2 ± 3.6	b
WIV	M	RDEL	3	23.7 ± 1.8	b
WIV	F	JON	5	23.6 ± 2.4	b
WIV	F	YDEL	5	26.8 ± 2.3	b
WIV	F	RDEL	5	25.3 ± 2.1	b

[a] SII = second generation (summer color morph), WIV = fourth generation (winter color morph).

[b] M = male, F = female.

[c] JON = Jonathan cultivar, YDEL = yellow delicious cultivar, RDEL = red delicious cultivar.

[d] Means followed by the same letter are not significantly different, $P \leq .01$.

analysis because they displayed atypical ovipositional patterns and/or unsuccessful mating attempts. Linear regression analyses for each rearing temperature, 18°, 22°, and 24°C, were performed on data collected for all females that met the above criteria. Analysis of variance indicated no significant differences between pupal weights and between fecundities for the 2 replications conducted under similar fluctuating temperatures. Therefore, both pupal weights and fecundities were pooled for all individuals reared under like treatments (temperatures). The mean pupal weights and corresponding fecundities are 18.08 mg and 262.71 eggs at 18°C, 18.03 mg and 274.00 eggs at 22°C, and 17.67 mg and 276.43 eggs at 24°C. Regression equations (fecundity as a linear function of pupal weight) were constructed for each temperature (Table 8). While the mean fecundities for each treatment are very similar, comparison of the regression equations indicates that the females reared at 22°C had a greater increase in fecundity for comparable increases in weight over the 18° and the 24°C reared females. This may indicate that 22°C approaches conditions that support optimal oviposition and, therefore, total fecundity. However, due to the high variability in fecundity and the lack of significance between treatment fecundities and pupal weights, a combined treatment equation was developed. This equation was constructed from 44 paired data points (Table 8, combined). Approximately 74% of the variability found in the observed fecundities can be explained by the equation, $Y = -212.42 + 26.92\ (X)$, where X = pupal weight in mg and Y = fecundity per female.

Table 8. Fecundity of laboratory reared females as a linear function of pupal weight (mg)

Treatments	N	Regression Equation	R^2
18°C[a]	17	Y = -171.51 + 24.02(X)	.85
22°C[b]	13	Y = -529.55 + 44.58(X)	.89
24°C[c]	14	Y = -145.95 + 23.90(X)	.69
Combined[d]	44	Y = -212.42 + 26.92(X)	.74

[a] Individuals reared and held as adults at a mean temperature of 18°C (12 hrs. at 24°C and 12 hrs. at 12°C) under a 16L/8D photoperiod.

[b] Individuals reared and held as adults at a mean temperature of 22°C (12 hrs. at 27°C and 12 hrs. at 16°C) under a 16L/8D photoperiod.

[c] Individuals reared and held as adults at a mean temperature of 24°C (12 hrs. at 31°C and 12 hrs. at 17°C) under a 16L/8D photoperiod.

[d] Individuals reared and held as adults at mean temperatures of 18°, 21°, or 24°C under a 16L/8D photoperiod.

3. Ovipositional pattern

If photophases entrain calling and temperatures promote mating, then oviposition will occur at dusk (1800 - 2100 CDST) under favorable environmental conditions. Under controlled laboratory conditions, temperature has an effect upon the ovipositional rate. While ovipositional rates on a daily basis for individuals held under 24° and 22°C appear to be similar, the ovipositional rates for those individuals held at 18° and 15°C are considerably less (Figure 13. A, B). Individuals reared at 15°C experienced temperatures of 10°C during the ovipositional period. While oviposition of viable eggs was possible under this temperature regime, the ovipositional pattern (Figure 13) was not typical of the ovipositional pattern of moths experiencing more optimal temperatures (18°-24°C). Females reared at 15°C oviposited a peak mean number of eggs per female per day on day 4 post emergence, while 18°, 22°, and 24°C reared females deposited their peak numbers of eggs on day 2 post emergence. Individuals reared under a 12°C mean fluctuating temperature (ovipositional activity period temperature = 7°C) were not included in the analysis. Because of the low mating success rate and the abnormal ovipositional pattern displayed by these females, it appears that a 7°C ovipositional period temperature is below the ovipositional temperature threshold.

The curves of the mean cumulative percentage oviposition of the cohorts versus a cumulative T.U. scale developed for each treatment (temperature) are not significantly different from each other (Figure 14). They can be expressed adequately by a combined equation, $Y = -.56 + .30 \ln (X)$, ($R^2 = .96$) where X = the T.U. accumulation daily post mating and Y = the predicted cumulative percentage oviposition (Table 9).

Table 9. Predicted cumulative percentage oviposition as a log function of thermal units accumulated daily post mating

Treatments	N	Regression Equation	R^2
15°C[a]	3	Y = -.61 + .32 ln(X)	.99
18°C[b]	22	Y = -.51 + .28 ln(X)	.99
22°C[c]	13	Y = -.60 + .31 ln(X)	.99
24°C[d]	12	Y = -.69 + .33 ln(X)	.99
Combined[e]	47	Y = -.56 + .30 ln(X)	.96

[a] Individuals reared and held as adults at a mean temperature of 15°C (12 hrs. at 20°C at 20°C and 12 hrs. at 10°C) under a 16L/8D photoperiod.

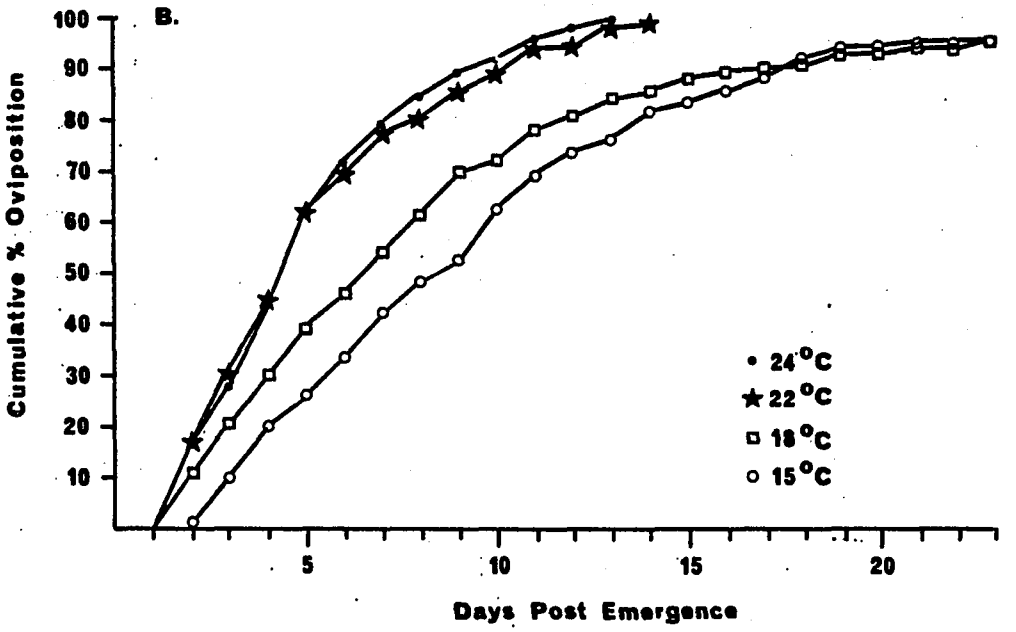
[b] Individuals reared and held as adults at a mean temperature of 18°C (12 hrs. at 24°C and 12 hrs. at 12°C) under a 16L/8D photoperiod.

[c] Individuals reared and held as adults at a mean temperature of 22°C (12 hrs. at 27°C and 12 hrs. at 16°C) under a 16L/8D photoperiod.

[d] Individuals reared and held as adults at a mean temperature of 24°C (12 hrs. at 31°C and 12 hrs. at 17°C) under a 16L/8D photoperiod.

[e] Individuals reared and held as adults at mean temperatures of 15°, 18°, 22°, or 24°C under a 16L/8D photoperiod.

Figure 13. Graphs of the ovipositional pattern characteristic of summer females held at 4 rearing temperatures: (A.) Mean number of eggs oviposited per female during each day, post emergence, at 24°, 22°, 18°, and 15°C; (B.) cumulative percentage oviposition for each day, post emergence, at 24°, 22°, 18°, and 15°C


B.
Cumulative % Oviposition
100
90
80
70
60
50
40
30
20
10
5
10
15
20
Days Post Emergence
• 24°C
★ 22°C
□ 18°C
○ 15°C

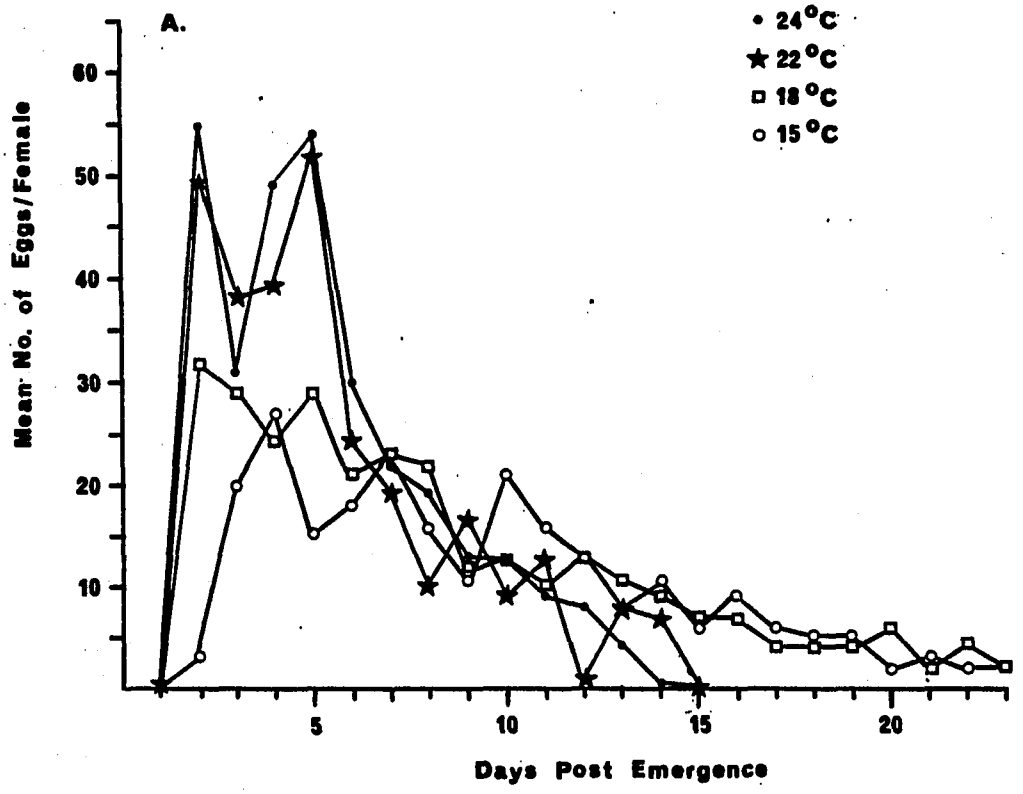
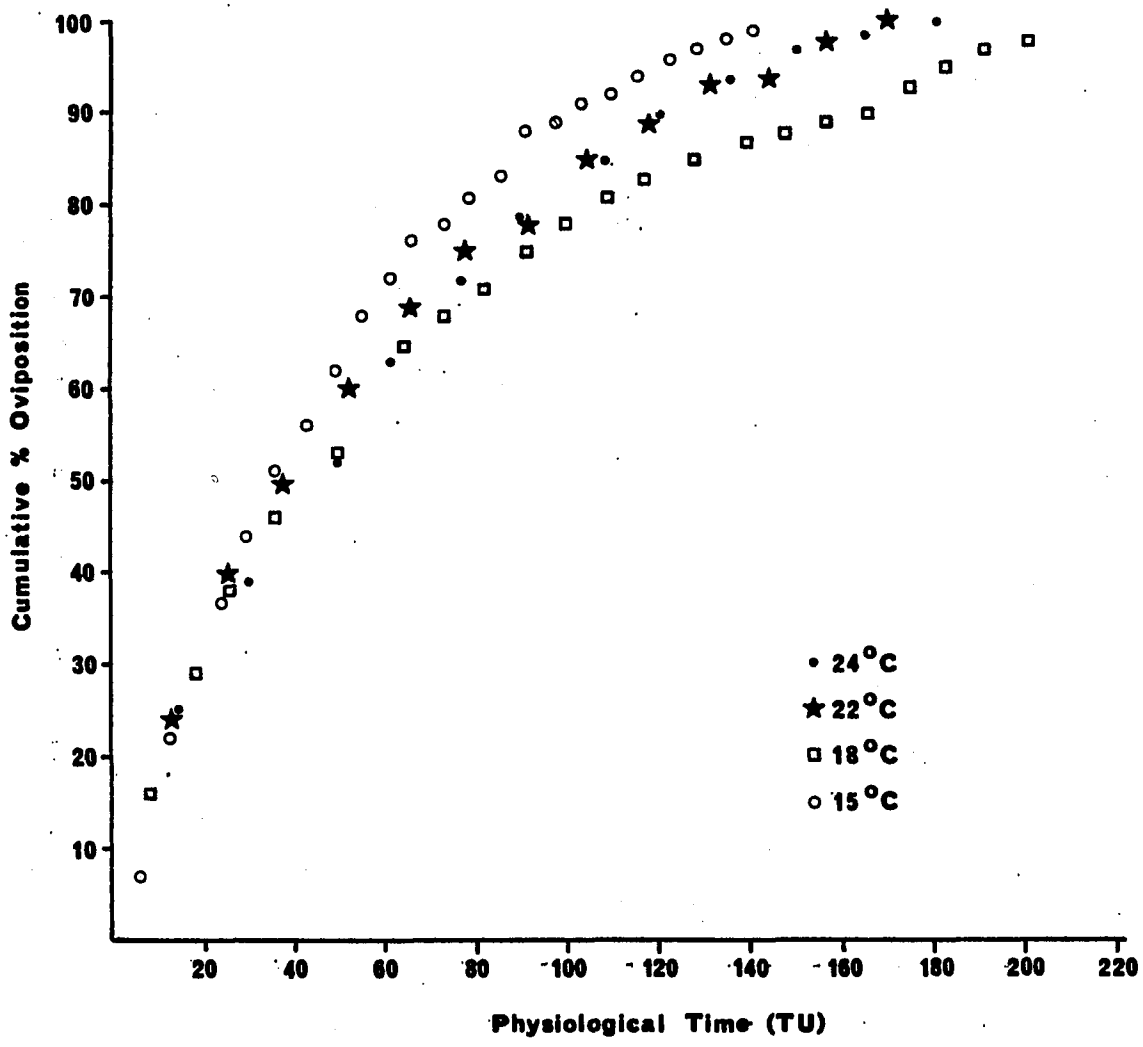

A.
Mean No. of Eggs/Female
60
50
40
30
20
10
5
10
15
20
Days Post Emergence
• 24°C
★ 22°C
□ 18°C
○ 15°C

Figure 14. Cumulative percentage oviposition plotted on a T.U. scale for moths held at 24°, 22°, 18°, and 15°C


Cumulative % Oviposition
100
90
80
70
60
50
40
30
20
10
20
40
60
80
100
120
140
160
180
200
220
Physiological Time (TU)
• 24°C
★ 22°C
□ 18°C
○ 15°C

Mean field temperatures during the ovipositional period (1800 CDST) were 26.24°C for SI, 26.53°C for SII, 28.58°C for SIII, 18.78°C for fall WIV, and 14.17°C for spring WIV generation. All adult flights experience temperatures that would promote successful oviposition. Spring WIV moths may display an ovipositional pattern atypical for the later summer generations because of the marginal temperatures experienced during the ovipositional period.

The effect of additional environmental conditions, e.g., wind velocity, cloud cover, precipitation, barometric pressure, and humidity, upon the ovipositional pattern has not been investigated. Field observations indicate that spring environmental conditions are more variable than summer or fall conditions (Table 10). The standard deviations found for each environmental variable give some indication of the seasonal variability associated with each environmental condition.

4. Ovipositional site preferences

Oviposition of SI eggs by the overwintering WIV females occurs just prior to bud break during the green tip stage of apple tree phenology. During this stage, the vegetative buds show green coloration, but the leaves remain furled. Consequently, WIV females oviposit on the bark of the tree and egg eclosion is synchronized closely with bud break. The summer females preferentially oviposit on the leaves. Based on field observations, the summer females oviposited more eggs within the terminal regions of the tree, the regions where succulent growth was available for larval consumption. In order to determine which regions of the canopy are

Table 10. Environmental conditions monitored during the ovipositional activity period of the adult flights (1978)

Environmental Condition	SI	SII	SIII	WIV (fall)
°C (1830 CDST)				
$\bar{x}$	26.24	26.53	28.58	18.78
S.D.	4.09	3.47	3.44	5.08
Wind Velocity				
$\bar{x}$ (kph)	24.14	16.50	21.63	18.15
S.D.	9.93	9.22	10.48	10.40
Barometric Pressure				
$\bar{x}$ (cm)	75.69	75.76	75.59	76.18
S.D.	0.36	0.28	0.36	0.56
Relative Humidity				
$\bar{x}$ (%)	54.77	63.50	57.27	57.20
S.D.	11.85	10.93	4.03	13.96

preferred as ovipositional sites and to determine the distribution of eggs within the canopy, an ovipositional site preference experiment was conducted according to the procedures described in Section III B.

Means of 21.78, 37.78, and 36.78 eggs/tree were recovered from ovipositional cages 1, 2, and 3, respectively. Based upon a predicted fecundity for 5 females, 1360.70 eggs, ($Y = -212.42 + 26.92(X)$; Y = fecundity/female, X = pupal weight; X for SIII pupae = 18.0 mg) the total number of eggs recovered per cage was 14, 25, and 24% of the predicted potential fecundity in cages 1, 2, and 3, respectively. Approximately 11% of the eggs recovered were oviposited within the dominant terminal region and 92% of these eggs were oviposited on the upper surface of the leaves (Table 11). Eggs located on side terminals represented approximately 33% of the total eggs recovered (Table 11). Because 44% of the eggs recovered were in the terminal regions, where less than 10% of the total leaf surface area is located, summer moths apparently prefer to oviposit upon leaves within these regions.

In order to determine if the ovipositional site preference relationships developed using confined moths would explain the egg distribution on uncaged trees, 36 trees were searched on each of 2 sampling dates for eggs, and egg frequencies by canopy regions were recorded. Under unconfined conditions, summer females oviposited 21% of the eggs within the dominant terminal region of the sampled trees (Table 12). This represents a 10% increase over the proportion of eggs oviposited within the dominant terminal region under caged conditions.

Table 11. Frequency of eggs oviposited, by 5 females per cage, in designated canopy regions

Region	Tree Number 1	2	3	4	5	6	7	8	9	Total	%
Cage 1											
Main terminal	1	2	0	3	4	3	1	0	3	17	9
Side terminals	3	3	1	0	5	11	4	6	3	36	18
Remainder	12	28	12	9	19	33	14	10	6	143	73
Total	16	33	13	12	28	47	19	16	12	196	
Cage 2											
Main terminal	11	9	5	2	3	5	1	2	1	39	11
Side terminals	21	6	20	57	10	12	3	2	2	133	39
Remainder	31	10	26	43	18	12	14	7	7	168	49
Total	63	25	51	102	31	29	18	11	10	340	
Cage 3											
Main terminal	6	6	1	4	5	3	5	3	3	36	11
Side terminals	60	2	11	26	5	7	5	4	0	120	36
Remainder	89	8	10	24	6	7	13	15	3	175	53
Total	155	16	22	54	16	17	23	22	6	331	

Table 12. Frequency of eggs oviposited, by unconfined SIII females, in designated canopy regions (Julian Dt. 254, 1978)

Variety[a]	Region	Tree Number 1	2	3	4	5	6	7	8	9	10	11	12	Total	%
JON															
	Main terminal	2	2	1	3	1	0	1	1	1	0	1	0	13	20
	Remainder	20	10	6	1	4	3	1	4	2	0	0	1	52	80
	Total	22	12	7	4	5	3	2	5	3	0	1	1	65	
YDEL															
	Main terminal	1	2	1	1	0	0	0	2	1	2	2	0	12	18
	Remainder	2	11	3	1	2	0	6	7	3	11	7	0	53	82
	Total	3	13	4	2	2	0	6	9	4	13	9	0	65	
RDEL															
	Main terminal	4	0	1	1	4	0	2	0	5	1	0	1	19	27
	Remainder	1	1	11	6	11	0	1	2	7	9	0	3	52	73
	Total	5	1	12	7	15	0	3	2	12	10	0	4	71	

[a] JON = Jonathan cultivar, YDEL = yellow delicious cultivar, RDEL = red delicious cultivar.

5. Adult longevity

Under field conditions, adult longevity is affected by 2 general classifications of mortality pressures, physiological (senility) and environmental. Senility appears to be a degree day function that allows adults to live longer lives under temperatures that promote slower rates of metabolism. Summer (orange) adult activities requiring major metabolic demands include calling, mating, and ovipositing. Calling, mating, and ovipositing of 90% of the laboratory fecundity associated with each of the 4 mean fluctuating rearing temperatures (15°, 18°, 22°, and 24°C) are accomplished during a 200-degree-day interval after emergence. Therefore, if 90% of the total fecundity is to be oviposited, moths reared at 15° and 18°C must live approximately 8 days longer than those held at 22° and 24°C. The longevity of the actively ovipositing females defines the length of the ovipositional period. The realization of the reproductive potential of the population is dependent upon the completion of this characteristic ovipositional period.

Under laboratory conditions where environmental mortality factors are eliminated, orange females, that have mated successfully, have a mean lifespan of 24.00 ± 1.82 days at 15°C, 18.67 ± 3.38 days at 18°C, 12.50 ± 2.0 days at 22°C and 12.94 ± 1.81 days at 24°C. Orange male lifespans averaged > 36 days at 15°C, > 24 days at 18°C, 20.12 ± 4.82 days at 22°C and 16.68 ± 3.80 days at 24°C. The mean lifespan of a gray female moth is approximately 3 times longer than the lifespan of an orange female under similar laboratory conditions. The mean lifespan of a gray

male moth is approximately 1.5 times longer than the lifespan of an orange male.

The environmental mortality factors are predominantly chronological functions that result from exposure to external pressures. The probability of a field moth dying of senility prior to succumbing to environmental mortality factors is extremely low.

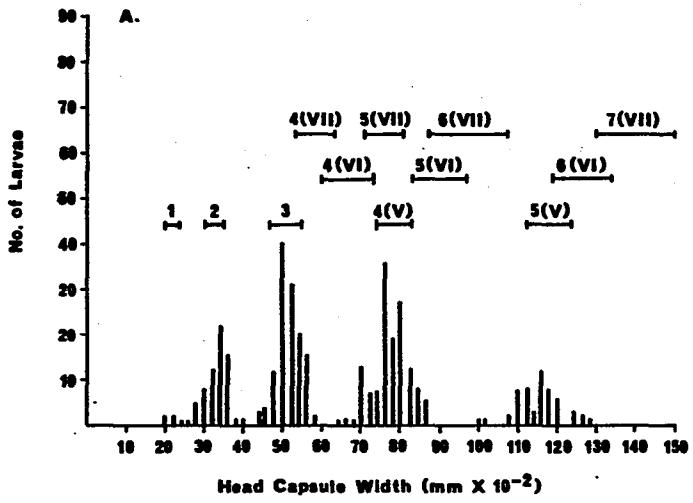
C. Developmental Polymorphism

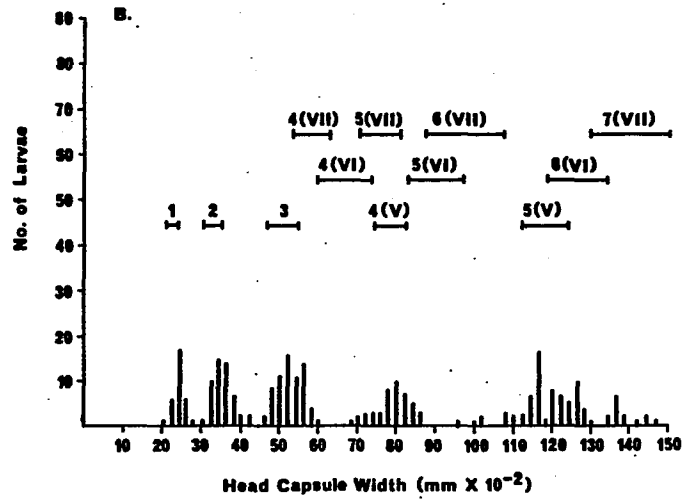
1. Determination of larval instars by head capsule measurements

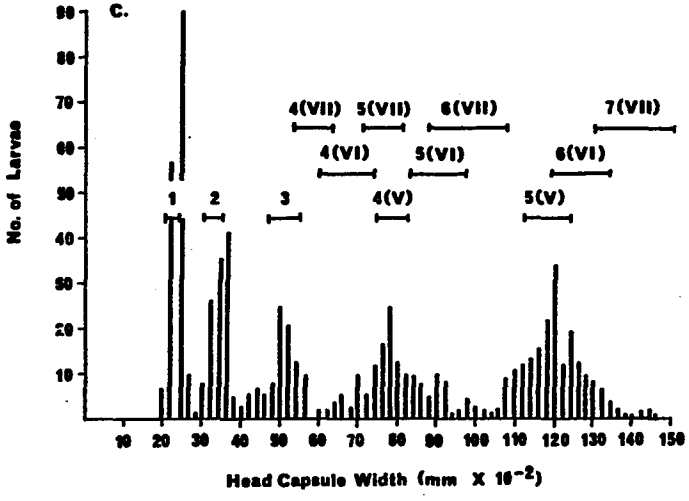
Frequency histograms (Figures 15 & 16) were developed from head capsule measurements taken from field collected larvae during the summers of 1977 and 1978. These histograms suggested that A. minuta larvae proceeded through 5 larval stadia. However, by examining the frequency histograms developed for each generation, it became apparent that head capsule measurements of the later instars tended to be more variable as the season progressed. Each discrete peak (Figures 15 & 16) was assumed to represent the frequency of individuals occurring in each larval stadium. The first 3 peaks of each generation were easily discriminated. As the season progressed, additional peaks developed suggesting the occurrence of additional instars.

To determine the range of head capsule size within each instar, development of 1,080 individuals was followed in the laboratory. Three hundred sixty individuals were reared under constant rearing temperatures, and 720 individuals were reared under fluctuating temperatures. Only individuals that successfully pupated were utilized in the analysis.

Figure 15. Frequency histograms of the head capsule widths (mm x 10^{-2}) for field collected larvae (1977): (A.) SI generation; (B.) SII generation; (C.) SIII generation; (D.) WIV generation. Superimposed on each histogram are the head capsule widths ($\bar{x} \pm$ S.D.) of laboratory reared instars. (Roman numeral = mode of development, arabic numerical = instar number


A.
No. of Larvae
4(VII) 5(VII) 6(VII) 7(VII)
4(VI) 5(VI) 6(VI)
1 2 3 4(V) 5(V)
10 20 30 40 50 60 70 80 90 100 110 120 130 140 150
Head Capsule Width (mm X 10⁻²)


B.
No. of Larvae
4(VII) 5(VII) 6(VII) 7(VII)
4(VI) 5(VI) 6(VI)
1 2 3 4(V) 5(V)
10 20 30 40 50 60 70 80 90 100 110 120 130 140 150
Head Capsule Width (mm X 10⁻²)


C.
No. of Larvae
4(VII) 5(VII) 6(VII) 7(VII)
4(VI) 5(VI) 6(VI)
1 2 3 4(V) 5(V)
10 20 30 40 50 60 70 80 90 100 110 120 130 140 150
Head Capsule Width (mm X 10⁻²)

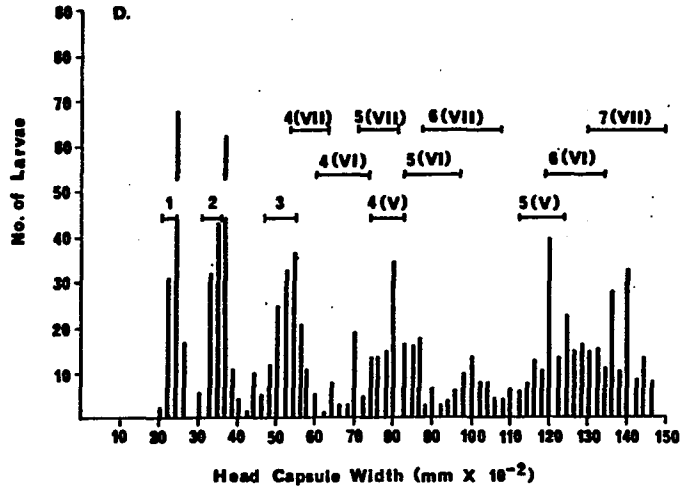
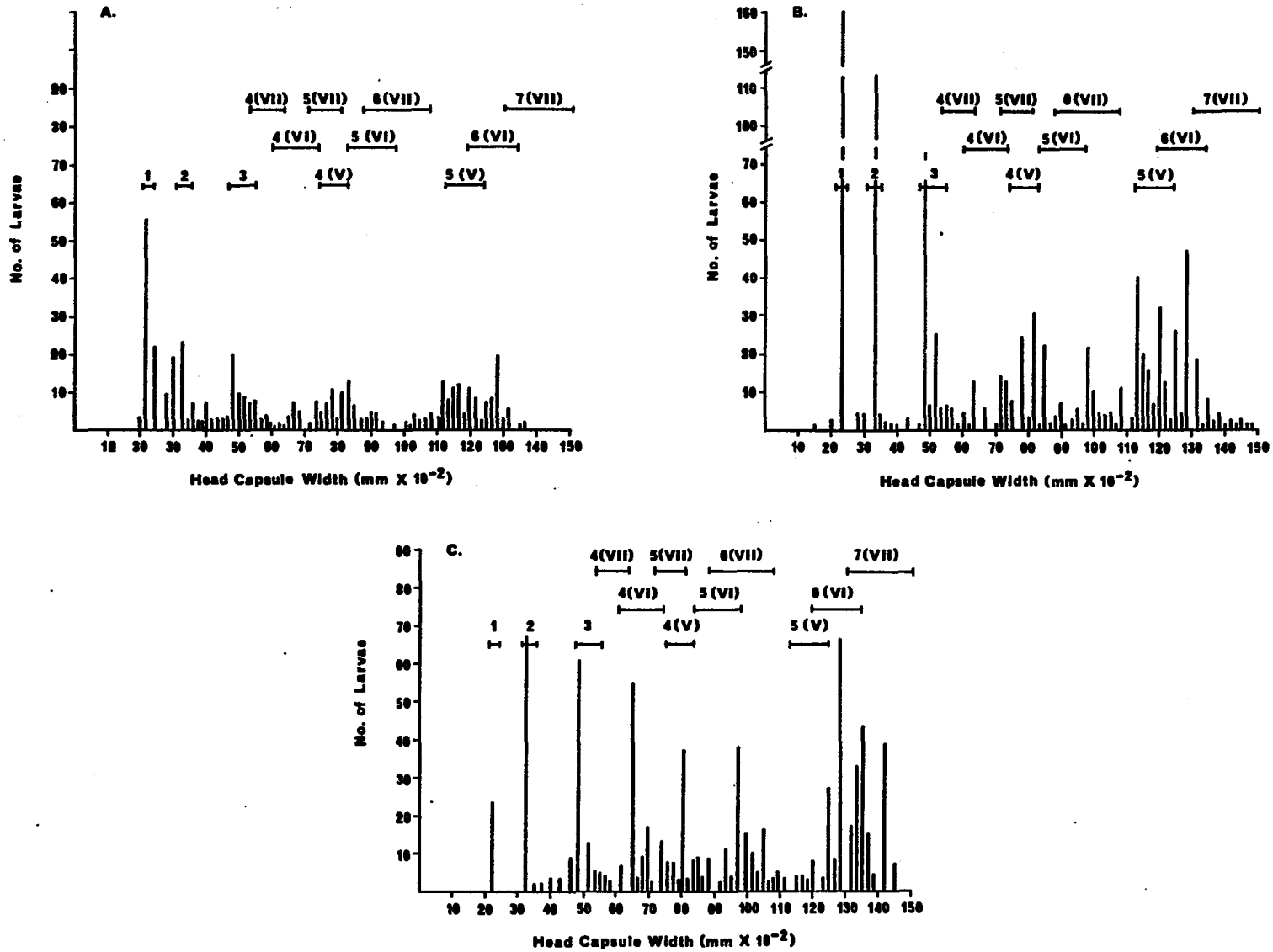

D.
No. of Larvae
4(VII) 5(VII) 6(VII) 7(VII)
4(VI) 5(VI) 6(VI)
1 2 3 4(V) 5(V)
10 20 30 40 50 60 70 80 90 100 110 120 130 140 150
Head Capsule Width (mm X 10⁻²)

Figure 16. Frequency histograms of the head capsule widths (mm x 10^{-2}) of field collected larvae (1978): (A.) SII generation; (B.) SIII generation; and (C.) WIV generation. Superimposed on each histogram are the head capsule widths ($\bar{x} \pm$ S.D.) of laboratory reared instars. (Roman numeral = mode of development, arabic numerals = instar number)


A.
B.
C.
No. of Larvae
Head Capsule Width (mm X 10⁻²)
1
2
3
4 (V)
5 (V)
4 (VI)
5 (VI)
6 (VI)
4(VII)
5(VII)
6(VII)
7(VII)

Head capsules from known instars were measured (Table 13). Under laboratory conditions, 3 modes of development occurred: a 5 instar mode, a 6 instar mode, and a 7 instar mode. When the population is classified by instar, the head capsule widths of the 5th and 6th instars are equivalent ($\bar{x}$ = 1.13 mm). When the population is classified by instar and sex, the head capsule widths of males and females of the 4th, 5th, and 6th instars reveal a trend towards sexual dimorphism. Female mean head capsules of the 4th, 5th, and 6th instars are .02, .05, and .06 mm wider, respectively, than male mean head capsules of the same instars. When the same laboratory population is classified by instar and mode of development (V, VI, or VII), the mean head capsule width of a 5th instar (Mode V) is 0.28 mm wider than the mean head capsule width of a 5th instar (Mode VI) that is 0.14 mm wider than the mean head capsule width of a 5th instar (Mode VII). Head capsule widths of the 7th instar, individuals pupating after completing 7 stadia, were not recorded. Based on trends, the mean head capsule widths of the final instars for the 3 modes of development equal or exceed 1.18 mm (Table 13).

Linear regressions of head capsule widths on instar number for each of the 3 developmental modes were developed (Table 14). Comparison of the slopes for the population by mode regressions, .1295 for the 7 instar mode, .1522 for the 6 instar mode, and .1772 for the 5 instar mode, indicates that individuals developing under a 5 instar mode have a greater increase in head capsule size for succeeding instars than do individuals developing under a 6 or 7 instar mode. Head capsule size was used as an index of body size. Because the head capsule limits the maximum size of

Table 13. Mean head capsule widths (mm) of laboratory reared larvae grouped by 1) population, 2) population by sex, 3) population by mode, and 4) population by sex and mode

Group	Instar		N	Mean ± S.D.
Population				
	I		549	0.23 ± 0.015
	II		560	0.33 ± 0.021
	III		563	0.51 ± 0.037
	IV		568	0.77 ± 0.060
	V		490	1.13 ± 0.122
	VI		22	1.13 ± 0.172
	VII		-	
Population by sex	I	Male	271	0.23 ± 0.015
		Female	273	0.23 ± 0.014
	II	Male	276	0.33 ± 0.021
		Female	278	0.33 ± 0.020
	III	Male	275	0.50 ± 0.036
		Female	283	0.51 ± 0.039
	IV	Male	280	0.76 ± 0.059
		Female	282	0.78 ± 0.060
	V	Male	237	1.11 ± 0.117
		Female	248	1.16 ± 0.123
	VI	Male	10	1.10 ± 0.179
		Female	12	1.16 ± 0.169
	VII		-	

Table 13. continued

Group	Instar	Mode V N	Mode V $\bar{x} \pm$ S.D.	Mode VI N	Mode VI $\bar{x} \pm$ S.D.	Mode VII N	Mode VII $\bar{x} \pm$ S.D.
Population by mode							
	I	475	0.23 ± 0.014	64	0.22 ± 0.015	10	0.22 ± 0.009
	II	486	0.34 ± 0.019	64	0.32 ± 0.019	10	0.31 ± 0.031
	III	488	0.52 ± 0.031	65	0.46 ± 0.037	10	0.42 ± 0.039
	IV	493	0.78 ± 0.035	65	0.67 ± 0.068	10	0.58 ± 0.054
	V	418	1.18 ± 0.057	63	0.90 ± 0.068	9	0.76 ± 0.051
	VI			12	1.26 ± 0.072	10	0.97 ± 0.101
	VII						-
Population mode by sex							
M[a]	I	234	0.23 ± 0.015	31	0.22 ± 0.015	6	0.22 ± 0.012
F[b]		237	0.23 ± 0.014	32	0.22 ± 0.016	4	0.22 ± 0.000
M	II	239	0.34 ± 0.020	31	0.31 ± 0.018	6	0.30 ± 0.020
F		242	0.34 ± 0.018	32	0.32 ± 0.020	4	0.31 ± 0.048
M	III	238	0.51 ± 0.029	31	0.46 ± 0.032	6	0.42 ± 0.020
F		246	0.52 ± 0.032	33	0.46 ± 0.042	4	0.43 ± 0.060
M	IV	243	0.77 ± 0.036	31	0.66 ± 0.061	6	0.57 ± 0.030
F		245	0.79 ± 0.032	33	0.68 ± 0.074	4	0.58 ± 0.085
M	V	202	1.15 ± 0.050	30	0.88 ± 0.061	5	0.75 ± 0.030
F		212	1.20 ± 0.054	32	0.91 ± 0.070	4	0.77 ± 0.074
M	VI			4	1.28 ± 0.123	6	0.98 ± 0.075
F				8	1.26 ± 0.041	4	0.96 ± 0.145
M	VII						-
F							-

[a] M = male.

[b] F = female.

Table 14. Linear regressions of head capsule widths in mm (Y) of laboratory reared individuals as a function of instar number (X)

Group		N	Regression	R^2	S.E.
Population		3111	log(Y) = -.8102 + .1716X	.97	.038
Population by sex					
M[a]		1556	log(Y) = -.8068 + .1693X	.97	.037
F[b]		1516	log(Y) = -.8136 + .1738X	.97	.039
Population by mode					
	V	2724	log(Y) = -.8183 + .1772X	.99	.025
	VI	328	log(Y) = -.7988 + .1522X	.98	.035
	VII	59	log(Y) = -.7742 + .1295X	.97	.039
Population mode by sex					
M	V	1363	log(Y) = -.8145 + .1748X	.98	.025
	VI	158	log(Y) = -.7958 + .1502X	.98	.030
	VII	35	log(Y) = -.7782 + .1301X	.99	.025
F	V	1327	log(Y) = -.8221 + .1796X	.99	.024
	VI	165	log(Y) = -.8015 + .1537X	.98	.037
	VII	24	log(Y) = -.7682 + .1286X	.95	.053

[a] M = male.

[b] F = female.

each instar, it was assumed that if the growth rate of the head capsule increased then the growth rate of the entire larva during the intermolt period also would increase. Stress factors acting directly on the larva or indirectly on the host plant, could decrease the optimal rate of growth. The 6 and 7 instar developmental modes found in both the laboratory and the field are probably caused by larval exposure to various stress factors. Under laboratory conditions, 100% of 46 surviving individuals reared at 22°C (constant temperature) followed the 5 instar developmental mode indicating that 22°C is a favorable temperature for rapid growth. As the temperature deviations increased from 22°C, increasing frequencies (30 - 100%) of individuals assumed the 6 or 7 instar developmental mode (Table 15). The effect of photoperiod upon the developmental mode was evaluated. The 2 photoperiod regimes (12L/12D, 16L/8D) used in the laboratory rearings had no effect upon the percentage of individuals in each developmental mode.

2. Critical size

For many lepidopterous insects, pupation does not occur until the larva reaches a minimum threshold or critical size. The number of larval molts characteristic of the species can vary, but once the larva exceeds this pre-coded critical size, pupation will occur. Graphic displays of the head capsule widths ($\bar{x} \pm$ S.D.) of 4th, 5th, and 6th instars under developmental modes V, VI, and VII were developed (Figure 17). Based upon the critical size theory, the final instars of all 3 developmental modes must exceed the critical size. A 5th instar (Mode V)

Table 15. Frequency of laboratory reared individuals developing under a 5, 6, or 7 instar developmental mode

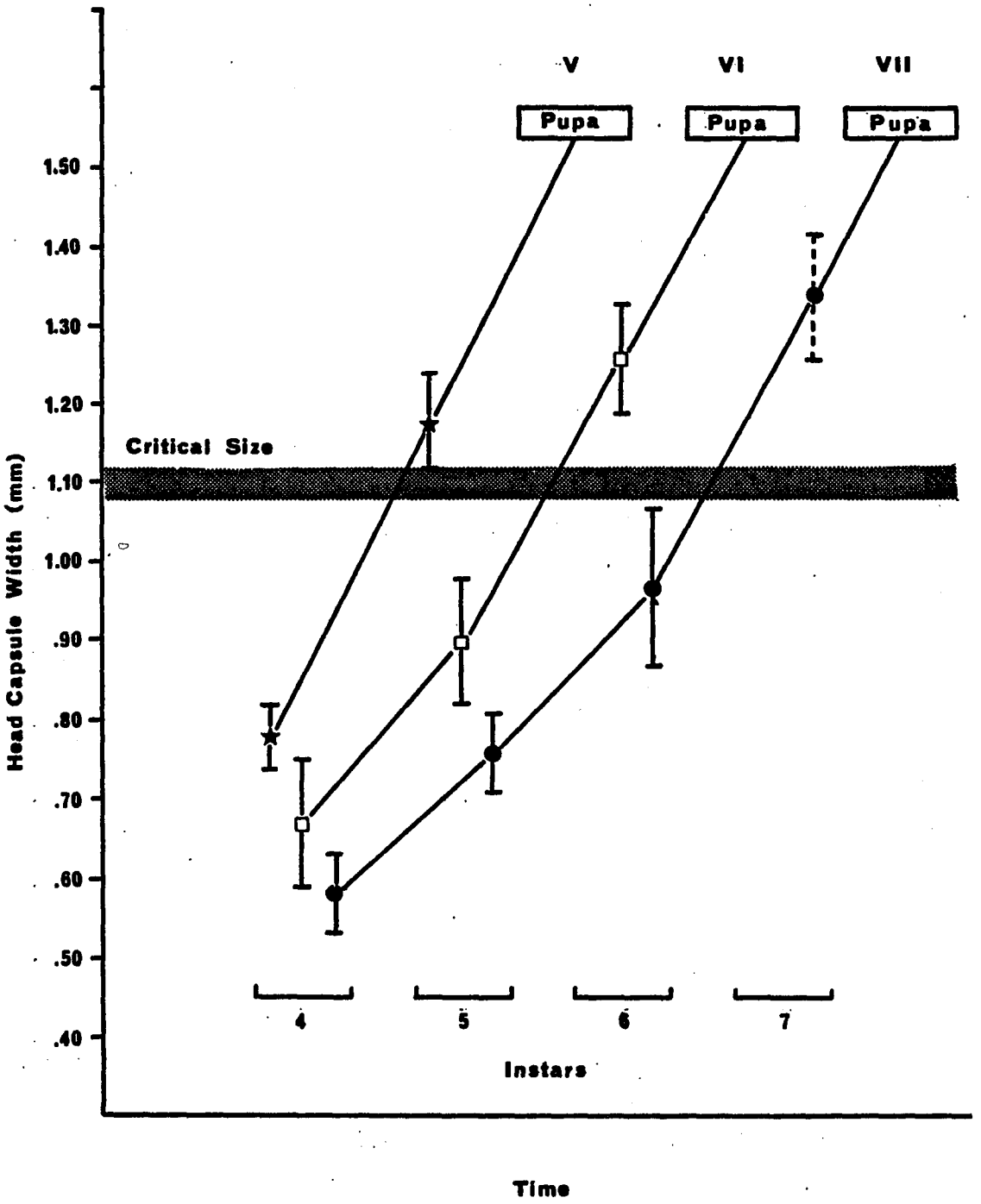
Const. Temp.	N		Developmental Mode[a] V	VI	VII
13°C	20	N[b]	0	16	4
		%[c]	0	80	20
15°C	35	N	13	20	2
		%	37	57	6
17°C	37	N	26	10	1
		%	70	27	3
22°C	46	N	46	0	0
		%	100	0	0
27°C	14	N	3	7	4
		%	21	50	29

[a] V = 5 instar developmental mode, VI = 6 instar developmental mode, VII = 7 instar developmental mode.

[b] N = frequency.

[c] % = proportion of the individuals reared under the same temperature which pupate after the 5th, the 6th, or the 7th stadium.

Figure 17. Mean head capsule width (± S.D.) for larval instars 4, 5, 6, and 7 under a V, VI and VII instar mode of development and the graphic determination of the critical size for pupation


V
VI
VII
Pupa
Pupa
Pupa
1.50
1.40
1.30
1.20
Critical Size
1.10
1.00
.90
.80
.70
.60
.50
.40
Head Capsule Width (mm)
4
5
6
7
Instars
Time

has a head capsule size range ($\bar{x} \pm$ S.D.) of 1.12 - 1.24 mm. The head capsule width of a 5th instar (Mode V) is smaller than the head capsule width of a 6th instar (Mode VI) and a 7th instar (Mode VII). Therefore, the critical size (1.10 mm) must be slightly less than the head capsule width of the smallest final instar (1.12 mm). Under a 5 instar mode of development, a final instar reaches a mean head capsule size of 1.18 mm, approximately 0.08 mm more than the critical size. A 5th instar under a 6 or 7 instar mode has a mean head capsule width of 0.90 mm and 0.76 mm, respectively. Supernumerary molts are necessary in order for the final instar to exceed the 1.10-mm critical size.

3. Developmental mode classification criterion

A discriminant model or classification criterion was developed from 640 head capsule measurements of laboratory reared larvae of known sex, instar and mode of development. Eighty percent of this population belonged to the 5 instar mode of development, 14% belonged to the 6 instar mode, and 6% belonged to the 7 instar mode. The discriminant function classified 65% of this laboratory population under the 5 instar mode, 19% under the 6 instar mode, and 16% under the 7 instar mode. Approximately 30% of the population was misclassified. This discriminant model based on head capsule size and sex was used to classify field individuals. After classifying each individual, the proportions of the sample field populations belonging to each developmental mode was calculated (Table 16). During the spring and summer generations (SI, SII, SIII), the greatest proportion of the population proceeded through a 5 instar developmental

Table 16. Proportion of the field population developing under a 5 instar, a 6 instar, and a 7 instar developmental mode

Generation	%[a] mode V		% mode VI		% mode VII	
	1977	1978	1977	1978	1977	1978
1	70		8		22	
2	53	44	27	31	20	25
3	58	47	25	28	16	25
4	35	12	25	37	40	51

[a] Percentages based on the discriminant function developed to classify individuals into instars based on head capsule size and sex.

mode, as illustrated by the 5 distinct peaks in Figures 15 & 16. Approximately 65% of the individuals belonging to the 1977 WIV generation and 88% of the individuals belonging to the 1978 WIV generation assumed a slower rate of growth shifting to a 6 or 7 instar developmental mode.

4. Environmental stress and its effect on developmental modes

The environmental factors that stimulate the change in developmental modes are unknown. It seems that seasonal changes in the apple foliage lower the nutritional value of the leaves. Rapid larval growth rates maintained by feeding on succulent new foliage in the spring cannot be maintained in the fall. It is suspected that the nitrogen content of the leaves, that drops from 3.512% in May to 1.617% in October (Thomas 1927), and the decreasing water content of the foliage contribute to the slowed developmental rate. This shift to a prolonged larval period is probably of adaptive significance to the overwintering population. Despite the slower growth rate, final instar larvae of the 6 and 7 instar modes are larger than the final instars of a 5 instar mode. These larger larvae develop into larger adults that probably possess greater energy reserves promoting a higher overwintering survival rate.

D. Developmental Models

1. Thermal unit models

Thermal unit models of development were constructed for both the summer and the winter color morphs under the 5 and the 6 instar devel-

opmental modes. Laboratory cohorts were reared under 5 fluctuating temperature regimes and 4 constant temperature regimes. The duration of each life stage was recorded for all individuals that successfully pupated and these data summarized as mean durations of each developmental stage for each color morph. The durations of the egg stage, the 1st stadium, the 2nd stadium, and the 3rd stadium are expressed as proportions of the egg through 3rd stadial period while the 4th stadium, the 5th stadium, the 6th stadium and the pupal stage are expressed as proportions of the 4th stadium through the pupal period. These mean durations were calculated from data collected from constant temperature rearings (Tables 17 & 18). Similar data collected from fluctuating temperature rearings were summarized but, because only a few individuals deviated from the 5 instar mode, only the 5 instar mode was summarized (Table 19).

Analysis of variance of the unweighted means of the reciprocal of developmental time (in days) of the egg stage, the larval stages, the pupal stage, and the egg to adult lifespan for individuals reared under constant temperatures and developing under a 5 instar mode indicated that rearing temperature had a significant effect upon duration (egg stage, $P < .01$, $F = 6773.46$; larval stage, $P < .01$, $F = 1826.46$; pupal stage, $P < .01$, $F = 2077.49$; egg to adult lifespan, $P < .01$, $F = 4789.41$). Similar results were obtained for individuals developing under a 6 instar mode and individuals reared under fluctuating temperatures. The exposure to different photoperiods (16L/8D, 12L/12D) resulted in a significant difference in the reciprocal of developmental time for the egg stage (mode 5, $P < .01$, $F = 274.54$; mode 6, $P < .01$, $F = 134.71$), the pupal stage

Table 17. Mean durations (in days and proportions) of developmental stages of laboratory reared summer and winter color morphs under a 5 instar developmental mode (constant temperature)

Temperature	Mode	N		Egg	1st	2nd	3rd
15°C	Smode V[a]	9	$\bar{x}$[b]	16.11	7.55	6.00	6.00
			%[c]	.45	.21	.17	.17
	Wmode V[d]	4	$\bar{x}$	15.00	8.00	6.50	6.25
			%	.42	.22	.18	.17
17°C	Smode V	11	$\bar{x}$	12.54	6.54	4.45	5.91
			%	.42	.22	.15	.20
	Wmode V	15	$\bar{x}$	11.00	7.67	5.00	5.07
			%	.38	.27	.17	.18
22°C	Smode V	22	$\bar{x}$	7.00	3.91	3.13	2.82
			%	.41	.23	.18	.17
	Wmode V	24	$\bar{x}$	6.33	4.21	2.75	3.12
			%	.39	.26	.17	.19
27°C	Smode V	3	$\bar{x}$	5.00	2.67	2.33	2.67
			%	.39	.21	.18	.21
	Wmode V		$\bar{x}$	-	-	-	-
Mean	Smode V		%	.42	.22	.17	.19
	Wmode V		%	.40	.25	.17	.18

[a] Individuals developing under a summer color morph scheme and pupating after 5 larval stadia.

[b] $\bar{x}$ = mean duration in days.

[c] % = mean duration of a developmental stage expressed as a proportion of the total duration of egg through 3rd stadium or of 4th stadium through pupal stage.

[d] Individuals developing under a winter color morph scheme and pupating after 5 larval stadia.

Total	4th	5th	N	Pupa	Total
35.66	7.89	11.11	8	20.25	39.25
	.20	.28		.51	
35.75	8.75	10.00	3	21.00	38.75
	.20	.26		.54	
29.44	6.73	11.36	10	16.00	34.09
	.20	.33		.47	
28.74	6.00	9.93	13	17.38	33.31
	.18	.30		.52	
16.86	4.27	6.82	19	9.47	20.56
	.21	.33		.46	
16.41	4.08	7.25	21	14.62	25.95
	.16	.28		.56	
12.67	4.00	6.33	2	8.50	18.83
	.21	.34		.45	
-	-	-		-	-
	.20	.32		.47	
	.18	.28		.54	

Table 18. Mean durations (in days and proportions) of developmental stages of laboratory reared summer and winter color morphs under a 6 instar developmental mode (constant temperature)

Temperature	Mode	N		Egg	1st	2nd	3rd
13°C	Smode VI[a]	7	$\bar{x}$[b]	20.28	11.28	9.14	10.71
			%[c]	.39	.22	.18	.21
	Wmode VI[d]	9	$\bar{x}$	20.11	13.55	12.55	10.78
			%	.35	.24	.22	.19
15°C	Smode VI	10	$\bar{x}$	16.10	7.70	6.70	6.70
			%	.43	.21	.18	.18
	Wmode VI	10	$\bar{x}$	15.70	7.60	7.60	7.30
			%	.41	.20	.20	.19
17°C	Smode VI	5	$\bar{x}$	13.40	7.60	5.20	5.80
			%	.42	.24	.16	.18
	Wmode VI	5	$\bar{x}$	11.40	8.20	5.60	5.80
			%	.37	.26	.18	.19
27°C	Smode VI	7	$\bar{x}$	5.00	3.14	3.14	2.71
			%	.36	.22	.22	.19
	Wmode VI		$\bar{x}$	-	-	-	-
Mean	Smode VI		%	.42	.22	.18	.19
	Wmode VI		%	.38	.23	.20	.19

[a] Individuals developing under a summer color morph scheme and pupating after 6 larval stadia.

[b] $\bar{x}$ = mean duration in days.

[c] % = mean duration of a developmental stage expressed as a proportion of the total duration of egg through 3rd stadium or of 4th stadium through pupal stage.

[d] Individuals developing under a winter color morph scheme and pupating after 6 larval stadia.

Total	4th	5th	6th	N	Pupa	Total
51.41	10.28	13.00	20.43	5	17.40	61.11
	.17	.21	.33		.28	
56.99	10.55	12.22	16.67	6	17.17	56.61
	.18	.21	.29		.30	
37.20	6.60	6.60	10.40	8	22.00	45.60
	.14	.14	.23		.48	
38.20	6.80	6.60	12.30	6	23.00	48.70
	.14	.13	.25		.47	
32.00	5.00	6.80	11.40	5	18.80	42.00
	.12	.16	.27		.45	
31.00	5.60	6.20	8.80	5	18.33	38.93
	.14	.16	.23		.47	
13.99	2.71	3.71	7.00	7	8.50	21.92
	.12	.17	.32		.39	
-	-	-	-		-	-
	.14	.17	.29		.40	
	.15	.17	.26		.41	

Table 19. Mean durations (in days and proportions) of the developmental stages of laboratory reared summer and winter color morphs under a 5 instar developmental mode (fluctuating temperature)

Fluct. Temp.	Mode	N		Egg	1st	2nd	3rd
12°C	Smode V[a]	28	$\bar{x}$[b]	-	9.36	5.80	6.00
			%[c]				
	Wmode V[d]	27	$\bar{x}$	-	9.31	6.00	5.88
			%				
15°C	Smode V	28	$\bar{x}$	11.21	6.93	5.53	5.14
			%	.39	.24	.19	.18
	Wmode V	26	$\bar{x}$	11.12	7.65	5.85	5.04
			%	.37	.26	.20	.17
18°C	Smode V	22	$\bar{x}$	8.77	4.54	4.77	3.68
			%	.40	.21	.22	.17
	Wmode V	30	$\bar{x}$	8.80	5.10	3.80	3.50
			%	.42	.24	.18	.17
22°C	Smode V	35	$\bar{x}$	6.67	3.88	3.44	2.79
			%	.40	.23	.20	.17
	Wmode V	29	$\bar{x}$	6.00	4.33	3.37	3.41
			%	.35	.25	.20	.20
24°C	Smode V	25	$\bar{x}$	6.00	3.28	2.88	3.12
			%	.39	.21	.19	.20
	Wmode V	30	$\bar{x}$	6.00	3.16	3.00	2.81
			%	.40	.21	.20	.19
Mean	Smode V		%	.40	.22	.20	.18
	Wmode V		%	.39	.24	.20	.18

[a] Individuals developing under a summer color morph scheme and pupating after 5 larval stadia.

[b] $\bar{x}$ = mean duration in days.

[c] % = mean duration of a developmental stage expressed as a proportion of the total duration of egg through 3rd stadium or of 4th stadium through pupal stage.

[d] Individuals developing under a winter color morph scheme and pupating after 5 larval stadia.

Total	4th	5th	N	Pupa	Total
21.16	9.52	15.08	26	23.26	47.86
	.20	.32		.49	
21.19	8.61	15.65	23	23.84	48.10
	.18	.33		.50	
28.81	6.50	11.21	24	16.79	34.50
	.19	.32		.49	
29.66	6.00	10.15	20	18.95	35.10
	.17	.29		.54	
21.76	4.73	7.95	22	12.86	25.54
	.19	.31		.50	
21.20	4.21	7.13	29	18.31	29.65
	.14	.24		.62	
16.87	3.50	6.06	33	10.50	20.06
	.17	.30		.52	
17.11	3.63	8.22	23	16.95	28.80
	.13	.29		.59	
15.28	3.68	6.12	23	9.13	18.93
	.19	.32		.48	
14.97	3.55	6.77	28	16.59	26.91
	.13	.25		.62	
	.19	.31		.50	
	.15	.28		.57	

(mode 5, $P < .01$, $F = 873.42$) and the egg to adult lifespan (mode 5, $P < .01$, $F = 75.29$).

The reciprocals of developmental time (in days) of the egg to adult lifespan (measured at constant temperatures) for both color morphs (combined and separate), under the 5 and the 6 instar modes were each regressed on temperature (Table 20). Paired comparisons of the slopes of the linear regressions revealed significant differences for mode 5 versus mode 6 ($P < .01$, $T = 6.86$, d.f. = 107), summer mode 5 versus winter mode 5 ($P < .01$, $T = 3.86$, d.f. = 72) and summer mode 6 versus winter mode 6 ($P < .05$, $T = 2.11$, d.f. = 31). The threshold temperatures for development (X intercept) of the combined summer and winter color morphs for the mode 5 and the mode 6 regressions were 7.56°C and 5.85°C, respectively. The differences in the slopes and the intercepts of the regressions resulted from the variability associated with the durations of the 4th stadium, the 5th stadium, the 6th stadium, and the pupal stage. In order to eliminate some of the variability and to develop a single meaningful threshold temperature for both color morphs and all developmental modes, the threshold temperature for development (X intercept) was calculated by regressing the reciprocal of the duration of the egg through the 3rd stadium on temperature (Tables 21 & 22).

The threshold temperature for development used throughout this dissertation, 8.85°C, was obtained from the linear regression for both color morphs and both developmental modes under constant rearing temperatures. The 4.95°C threshold calculated from the linear regression for both color morphs (mode 5) under fluctuating rearing temperatures was

Table 20. Regression equations of the reciprocals (1/duration in days) of egg-to-adult development on temperature (°C) for laboratory individuals reared under constant temperatures

	Regression	R^2	Threshold (°C)
Combined developmental modes[a]	Y = -.0137 + .0017X	.93	8.06
Mode V[b]	Y = -.0136 + .0018X	.92	7.56
Smode V[c]	Y = -.0158 + .0019X	.95	8.32
Wmode V[d]	Y = -.0098 + .0015X	.93	6.53
Mode VI[e]	Y = -.0076 + .0013X	.98	5.85
Smode VI[f]	Y = -.0072 + .0012X	.98	6.00
Wmode VI[g]	Y = -.0104 + .0015X	.95	6.93

[a] Individuals developing under a summer or winter color morph scheme and pupating after 5 or 6 larval stadia.

[b] Individuals developing under a summer or winter color morph scheme and pupating after 5 larval stadia.

[c] Individuals developing under a summer color morph scheme and pupating after 5 larval stadia.

[d] Individuals developing under a winter color morph scheme and pupating after 5 larval stadia.

[e] Individuals developing under a summer or winter color morph scheme and pupating after 6 larval stadia.

[f] Individuals developing under a summer color morph scheme and pupating after 6 larval stadia.

[g] Individuals developing under a winter color morph scheme and pupating after 6 larval stadia.

Table 21. Regression equations of the reciprocals (1/duration in days) of egg through 3rd instar development on temperature (°C) for laboratory individuals reared under constant temperatures

Developmental Mode	Regression	R^2	Threshold (°C)
Combined developmental modes[a]	Y = -.0388 + .0044X	.84	8.85
Mode V[b]	Y = -.0444 + .0047X	.94	9.38
Smode V[c]	Y = -.0411 + .0045X	.95	9.06
Wmode V[d]	Y = -.0505 + .0051X	.93	9.95
Mode VI[e]	Y = -.0305 + .0038X	.99	8.10
Smode VI[f]	Y = -.0296 + .0037X	.99	7.94
Wmode VI[g]	Y = -.0306 + .0037X		8.17

[a] Individuals developing under a summer or winter color morph scheme and pupating after 5 or 6 larval stadia.

[b] Individuals developing under a summer or winter color morph scheme and pupating after 5 larval stadia.

[c] Individuals developing under a summer color morph scheme and pupating after 5 larval stadia.

[d] Individuals developing under a winter color morph scheme and pupating after 5 larval stadia.

[e] Individuals developing under a summer or winter color morph scheme and pupating after 6 larval stadia.

[f] Individuals developing under a summer color morph scheme and pupating after 6 larval stadia.

[g] Individuals developing under a winter color morph scheme and pupating after 6 larval stadia.

Table 22. Regression equations of the reciprocals (1/duration in days) of egg through 3rd instar development on temperature (°C) for laboratory individuals reared under fluctuating temperatures

Developmental Mode	Regression	R^2	Threshold (°C)
Combined developmental modes[a]	Y = -.0173 + .0035X	.93	4.95
Mode V[b]	Y = -.0178 + .0035X	.94	5.04
Smode V[c]	Y = -.0164 + .0034X	.92	4.76
Wmode V[d]	Y = -.0191 + .0036X	.95	5.30

[a] Individuals developing under a summer or winter color morph scheme and pupating after 5 or 6 larval stadia.

[b] Individuals developing under a summer or winter color morph scheme and pupating after 5 larval stadia.

[c] Individuals developing under a summer color morph scheme and pupating after 5 larval stadia.

[d] Individuals developing under a winter color morph scheme and pupating after 5 larval stadia.

well below the actual biological threshold, estimated to be approximately 10°C. Only when the daily high temperature exceeds the true biological threshold will development occur. The 4.95°C threshold would be applicable if the daily high exceeded the true biological threshold. When this occurs, the daily low temperature can drop below the biological threshold resulting in a mean daily temperature in the 4.95°C range. However, on days when the high temperature exceeds 4.95°C but is less than the biological threshold, development would not proceed. The 8.85°C threshold more nearly approximates the true biological threshold of development.

Frequency distributions of the duration (in T.U.s) of each life stage of laboratory individuals were constructed (Tables 23 - 33). The T.U. accumulations for individuals reared under constant temperatures were calculated by subtracting 8.85°C from the daily temperature and accumulating these differences for the duration (in days) of the life stage. Low temperatures for short durations probably arrest development rather than regress development. Therefore, if the daily temperature does not exceed the threshold, the daily temperature is set equal to 8.85°C and no T.U.s are accumulated. The T.U. accumulations for individuals reared under fluctuating temperatures were calculated by averaging the daily maximum and minimum temperatures, subtracting 8.85°C from the daily mean temperature, and accumulating these differences for the duration (in days) of the life stage. If the minimum temperature was less than 8.85°C, then the minimum temperature was set equal to 8.85°C. Likewise, if the daily mean temperature were less than 8.85°C, then no T.U.s were accumulated.

Table 23. Frequency distribution of the duration of the egg stage of laboratory reared individuals

Duration (T.U.)	16L/8D				12L/12D			
	Const.[a]		Fluct.[b]		Const.		Fluct.	
	Freq.	%	Freq.	%	Freq.	%	Freq.	%
70			22	19			23	19
75			12	10			11	9
80			26	22	19	18	50	42
85								
90	56	50	56	48	65	61	34	29
95								
100	33	29			15	14		
105	22	20			6	6		
110					1	1		
115	1	1						
Totals	112	100	116	99	106	100	118	99

[a] Const. = constant temperature rearings.

[b] Fluct. = fluctuating temperature rearings.

Table 24. Frequency distribution of the duration of the first stadium of laboratory reared individuals

Duration (T.U.)	16L/8D				12L/12D			
	Const.[a]		Fluct.[b]		Const.		Fluct.	
	Freq.	%	Freq.	%	Freq.	%	Freq.	%
20			1	0				
25								
30							1	0
35	2	3	38	14	3	4	26	9
40	4	5	18	7	1	1	14	5
45	11	14	80	29	3	4	88	30
50	14	18	9	3	7	9	21	7
55	36	46	87	32	36	47	68	23
60	1	1	28	10	1	1	22	8
65	3	4	7	3	16	21	36	12
70					1	1	1	0
75	7	9	4	1	8	10	10	3
80			2	1	1	1	3	1
85								
90			1	0				
95								
100								
105			1	0				
Totals	78	100	276	100	77	99	290	98

[a] Const. = constant temperature rearings.

[b] Fluct. = fluctuating temperature rearings.

Table 25. Frequency distribution of the duration of the second stadium of laboratory reared individuals

Duration (T.U.)	16L/8D				12L/12D			
	Const.[a]		Fluct.[b]		Const.		Fluct.	
	Freq.	%	Freq.	%	Freq.	%	Freq.	%
10								
15			2	1	1	1	1	0
20			8	3			9	3
25	3	4	28	10	5	7	42	15
30	2	3	36	13	1	1	28	10
35	15	20	67	25	8	11	79	28
40	25	34	40	15	28	37	39	14
45	7	9	52	19	7	9	67	23
50	4	5	1	0	7	9	4	1
55	15	20	28	10	19	25	13	5
60	1	1	7	3			4	1
65	1	1	4	1			1	0
70								
75	1	1						
Totals	74	98	273	100	76	100	287	100

[a] Const. = constant temperature rearings.

[b] Fluct. = fluctuating temperature rearings.

Table 26. Frequency distribution of the duration of the third stadium of laboratory reared individuals

Duration (T.U.)	16L/8D				12L/12D			
	Const.[a]		Fluct.[b]		Const.		Fluct.	
	Freq.	%	Freq.	%	Freq.	%	Freq.	%
10								
15							2	1
20			9	3			8	3
25	5	7	55	20	5	7	50	17
30	2	3	41	15			43	15
35	13	18	51	19	11	15	70	24
40	20	27	41	15	22	29	33	12
45	10	14	49	18	4	5	48	17
50	9	12			8	11		
55	13	18	13	5	24	32	25	9
60			11	4			6	2
65			1	0				
70								
75	2	3	1	0			1	0
80								
85								
90					1	1		
Totals	74	102	272	100	75	100	286	100

[a] Const. = constant temperature rearings.

[b] Fluct. = fluctuating temperature rearings.

Table 27. Frequency distribution of the duration of the fourth stadium (mode 5) of laboratory reared individuals

Duration (T.U.)	16L/8D				12L/12D			
	Const.[a]		Fluct.[b]		Const.		Fluct.	
	Freq.	%	Freq.	%	Freq.	%	Freq.	%
15								
20								
25			4	2			10	4
30			17	7			35	13
35			58	22			72	27
40	4	8	46	18	9	20	35	13
45	3	6	57	22	1	2	66	25
50	7	14	9	3	10	23	2	1
55	22	43	35	13	15	34	23	9
60			22	8			12	4
65	7	14	9	3	6	14	9	3
70								
75	7	14	2	1	2	5	4	1
80	1	2			1	2		
85								
90			2	1				
120							1	0
Totals	51	101	261	100	44	100	269	100

[a] Const. = constant temperature rearings.

[b] Fluct. = fluctuating temperature rearings.

Table 28. Frequency distribution of the duration of the fourth stadium (mode 6) of laboratory reared individuals

Duration (T.U.)	16L/8D				12L/12D			
	Const.[a]		Fluct.[b]		Const.		Fluct.	
	Freq.	%	Freq.	%	Freq.	%	Freq.	%
20								
25			1	13				
30	1	5	1	13	1	4	1	11
35	4	21			4	17	3	33
40	3	16			3	13	2	22
45	5	26	4	50	5	21	2	22
50	2	11			2	8		
55	3	16	1	13	9	38		
60			1	13				
65								
70								
75	1	5						
Totals	19	100	8	102	24	101	9	99

[a] Const. = constant temperature rearings.

[b] Fluct. = fluctuating temperature rearings.

Table 29. Frequency distribution of the duration of the fifth stadium (mode 5) of laboratory reared individuals

Duration (T.U.)	16L/8D				12L/12D			
	Const.[a]		Fluct.[b]		Const.		Fluct.	
	Freq.	%	Freq.	%	Freq.	%	Freq.	%
30								
35								
40							1	0
45			3	1			2	1
50			2	1			7	3
55	1	2	30	11	1	2	44	16
60	2	4	34	13	2	4	27	10
65	2	4	52	20	1	2	43	16
70	3	6	11	4	1	2	13	5
75	2	4	43	16	4	9	26	9
80	10	20	39	15	11	24	16	6
85	1	2	1	0			3	1
90	11	22	37	14	14	31	31	11
95								
100	6	12			2	4		
105	5	10	8	3	5	11	30	11
110	5	10						
115								
120			1	0	1	2	27	10
125	1	2						
130					1	2	2	1
135			1	0			2	1
140								
145	1	2			2	4		
150							1	0
Totals	50	100	262	98	45	97	275	101

[a] Const. = constant temperature rearings.

[b] Fluct. = fluctuating temperature rearings.

Table 30. Frequency distribution of the duration of the fifth stadium (mode 6) of laboratory reared individuals

Duration (T.U.)	16L/8D				12L/12D			
	Const.[a]		Fluct.[b]		Const.		Fluct.	
	Freq.	%	Freq.	%	Freq.	%	Freq.	%
15								
20								
25							1	11
30	1	5						
35	3	16			5	22	3	33
40							2	22
45	5	26	3	38	4	17		
50	3	16			5	22		
55	4	21	1	13	1	4		
60			4	50			1	11
65	1	5						
70								
75	2	11			5	22	1	11
80							1	11
85								
90					1	4		
95								
100								
105								
110					2	9		
Totals	19	100	8	101	23	100	9	99

[a] Const. = constant temperature rearings.

[b] Fluct. = fluctuating temperature rearings.

Table 31. Frequency distribution of the duration of the sixth stadium (mode 6) of laboratory reared individuals

Duration (T.U.)	16L/8D				12L/12D			
	Const.[a]		Fluct.[b]		Const.		Fluct.	
	Freq.	%	Freq.	%	Freq.	%	Freq.	%
45								
50	3	16						
55					2	8	3	33
60	4	21	1	13			1	11
65					3	13		
70	1	5			5	21		
75	1	5	1	13	1	4		
80	1	5	1	13	1	4	1	11
85	1	5			1	4		
90	2	11	4	50			2	22
95								
100	1	5			2	8		
105	1	5	1	13			1	11
110					1	4		
115								
120							1	11
125	3	16			1	4		
130								
135								
140								
145	1	5			1	4		
.								
165					5	21		
.								
200					1	4		
Totals	19	99	8	102	24	99	9	99

[a] Const. = constant temperature rearings.

[b] Fluct. = fluctuating temperature rearings.

Table 32. Frequency distribution of the duration of the pupal stage of laboratory reared summer color morphs (16L/8D)

Duration (T.U.)	Const.[a] Freq.	Const.[a] %	Fluct.[b] Freq.	Fluct.[b] %
85				
90			15	7
95			7	3
100			19	8
105	1	2	20	9
110	1	2	24	11
115	2	3	15	7
120	12	19	45	20
125	2	3	2	1
130	21	34	21	9
135	1	2	37	16
140	3	5		
145	8	13	12	5
150			8	4
155	7	11	2	1
160	1	2		
165	1	2		
170	1	2	1	0
175				
180				
185				
190				
195				
200				
205	1	2		
210				
Totals	62	102	228	101

[a] Const. = constant temperature rearings.

[b] Fluct. = fluctuating temperature rearings.

Table 33. Frequency distribution of the duration of the pupal stage of laboratory reared winter color morphs (12L/12D)

Duration (T.U.)	Const.[a] Freq.	%	Fluct.[b] Freq.	%	Duration (T.U.)	Const. Freq.	%	Fluct. Freq.	%
85			3	1	215	2	4		
90			2	1	220			1	0
95			4	2	225	1	2	5	2
100			4	2	230				
105			1	0	235			8	4
110			1	0	240			6	3
115			3	1	245				
120	1	2			250			9	4
125			9	4	255			14	7
130	5	9	13	6	260				
135			8	4	265			3	1
140	6	11	2	1	270	1	2	10	5
145	8	14	5	2	275			3	1
150					280				
155	5	9	7	3	285			4	2
160	1	2			290	2	4	1	0
165	1	2	16	8	295				
170	4	7	1	0	300			1	0
175			15	7	305			2	1
180			1	0	310	2	4		
185	5	9	15	7	315				
190			6	3	320			1	0
195	8	14	9	4	325	1	2		
200			2	1	330				
205					335				
210	3	5	11	5	340				
					345	1	2		
Totals						57	104	206	101

[a] Const. = constant temperature rearings.

[b] Fluct. = fluctuating temperature rearings.

These frequency distributions were summarized by listing the mean thermal units required for development under constant and fluctuating temperatures (Tables 34 & 35). The mean cumulative T.U.s required for egg to adult development (Mode 5) for the summer color morph are 507.74 T.U.s under constant temperatures and 456.51 T.U.s under fluctuating temperatures. Based upon laboratory rearings, individuals reared under fluctuating temperatures required 51.23 T.U.s less than individuals reared under constant temperatures. Under fluctuating temperatures, if the 12 hours of high temperatures correspond to the period of greatest larval feeding, digestion, and assimilation and the 12 hours of low temperatures correspond to the period of larval inactivity, development would proceed at a rate governed by the high temperature rather than the mean temperature. Based upon this hypothesis, individuals developing under constant temperatures would develop more slowly than individuals developing under an equivalent mean fluctuating temperature. The cumulative T.U.s required for egg to adult development (Mode 5) for the winter color morph are 506.97 and 523.29 T.U.s under constant and fluctuating temperatures, respectively. Unlike the summer color morph, development of the winter color morph under fluctuating temperatures requires 16.32 T.U.s more than development under constant temperatures. The difference in the duration of the pupal period for individuals reared under constant temperatures (153.19 T.U.s) and for individuals reared under fluctuating temperatures (180.18 T.U.s) accounts for most of the difference in T.U. accumulations.

Table 34. Thermal units required for development of the summer and winter color morphs under a 5 and a 6 instar developmental mode (constant temperature, developmental threshold temperature = 8.85°C)

Stage	Smode V[a]		Wmode V[b]		Smode VI[c]		Wmode VI[d]	
	T.U.s	Cum. T.U.s	T.U.s	Cum. T.U.s	T.U.s	Cum. T.U.s	T.U.s	Cum. T.U.s
Egg	95.65	95.65	89.32	89.32	100.47	100.47	91.72	91.72
1st	50.10	145.75	55.82	145.14	52.63	153.10	55.51	147.23
2nd	38.71	184.46	37.96	183.10	43.06	196.16	48.27	195.50
3rd	43.27	227.73	40.19	223.29	45.45	241.61	45.86	241.36
4th	56.57	284.30	51.06	274.35	44.60	286.21	42.59	283.95
5th	90.51	374.81	79.43	353.78	54.15	340.36	48.26	332.21
6th					92.38	432.74	73.82	406.03
Pupa	132.93	507.74	153.19	506.97	127.42	560.16	116.40	522.43
Total		507.74		506.97		560.16		522.43

[a] Individuals developing under a summer color morph scheme and pupating after 5 larval stadia.

[b] Individuals developing under a winter color morph scheme and pupating after 5 larval stadia.

[c] Individuals developing under a summer color morph scheme and pupating after 6 larval stadia.

[d] Individuals developing under a winter color morph scheme and pupating after 6 larval stadia.

Table 35. Thermal units required for development of the summer and winter color morphs under a 5 instar developmental mode (fluctuating temperature, developmental threshold temperature = 8.85°C)

Stage	Smode V[a]		Wmode V[b]	
	T.U.s	Cum. T.U.s	T.U.s	Cum. T.U.s
Egg	82.96	82.96	80.07	80.07
1st	45.63	128.59	49.27	129.34
2nd	41.48	170.07	41.06	170.40
3rd	37.33	207.40	36.96	207.36
4th	47.33	254.73	47.39	254.75
5th	77.22	331.95	88.46	343.21
Pupa	124.56	456.51	180.08	523.29
Total		456.51		523.29

[a] Individuals developing under a summer color morph scheme and pupating after 5 larval stadia.

[b] Individuals developing under a winter color morph scheme and pupating after 5 larval stadia.

2. Greenhouse verification of thermal unit models

In order to validate the thermal unit models, a greenhouse experiment was conducted using 72 newly eclosed 1st instar larvae. Thirty-six individuals were reared to adults under a 12L/12D photoperiod and 36 individuals were reared to adults under a 16L/8D photoperiod. The duration of each life stage was calculated on a thermal unit scale utilizing 8.85°C as the threshold temperature (TU = Tmax + Tmin)/2 - 8.85°C; if Tmin < 8.85°C then Tmin = 8.85°C). The mean cumulative thermal units required for development under the constant temperature and the fluctuating temperature models were compared with the mean cumulative thermal units required for development in the greenhouse verification experiment (Tables 36 & 37). When considering the summer 5 instar developmental mode, the fluctuating temperature model predicted adult emergence at 456.51 T.U.s, while the constant temperature model predicted adult emergence at 507.74 T.U.s. Adult emergence in the greenhouse verification experiment occurred after the accumulation of 464.81 T.U.s, 8.30 T.U.s more than the fluctuating temperature model and 42.93 T.U.s less than the constant temperature model. The fluctuating temperature model predicted adult emergence of winter moths of the 5 instar developmental mode at 523.29 T.U.s, and the constant temperature model predicted adult emergence at 506.97 T.U.s. Adult emergence of the gray moth in the greenhouse experiment occurred after the accumulation of 585.51 T.U.s, 62.22 T.U.s more than the fluctuating temperature model and 78.54 T.U.s more than the constant temperature model. Based upon these results, the thermal unit model constructed from fluctuating temperature rearings is used as the most reliable reference for further research.

Table 36. Comparison of the thermal unit models required for development of the summer color morph under a 5 instar developmental mode (developmental threshold temperature = 8.85°C)

Stage	Environmental Chamber		N	Greenhouse
	T.U.s (constant)[a]	T.U.s (fluctuating)[b]		T.U.s[c]
1st	145.75	128.59	27	151.61
2nd	184.46	170.07	27	183.52
3rd	227.73	207.40	27	218.69
4th	284.30	254.73	27	262.55
5th	374.81	331.95	27	336.97
Pupa	507.74	456.51	26	464.81

Pupa

Greenhouse T.U.s - T.U.s (fluctuating) — 8.30

Greenhouse T.U.s - T.U.s (constant) — 42.93

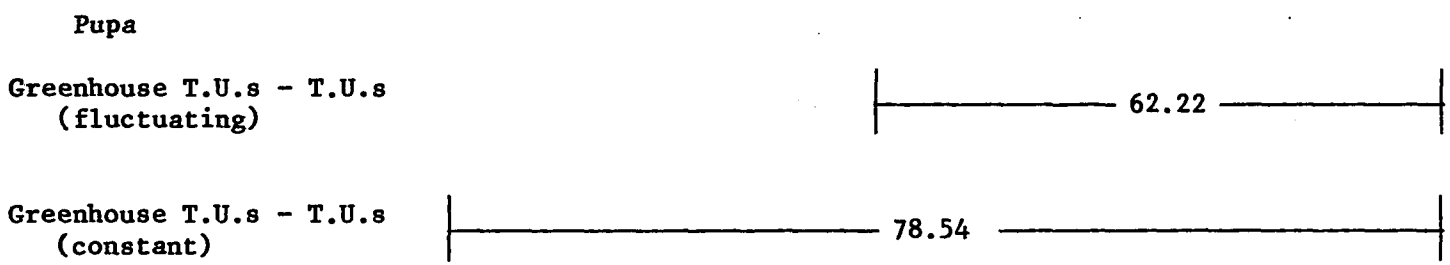
[a] T.U.s (constant) = thermal unit model constructed from data collected during constant temperature rearings.

[b] T.U.s (fluctuating) = thermal unit model constructed from data collected during fluctuating temperature rearings.

[c] Thermal units required for development in the greenhouse verification experiment.

Table 37. Comparison of the thermal unit models required for development of the winter color morph under a 5 instar developmental mode (developmental threshold temperature = 8.85°C)

Stage	Environmental Chamber		N	Greenhouse
	T.U.s (constant)[a]	T.U.s (fluctuating)[b]		T.U.s[c]
1st	145.14	129.34	13	140.61
2nd	183.10	170.40	13	179.48
3rd	223.29	207.36	13	220.61
4th	274.35	254.75	13	275.72
5th	353.78	343.21	12	374.75
Pupa	506.97	523.29	11	585.51



[a] T.U.s (constant) = thermal unit model constructed from data collected during constant temperature rearings.

[b] T.U.s (fluctuating) = thermal unit model constructed from data collected during fluctuating temperature rearings.

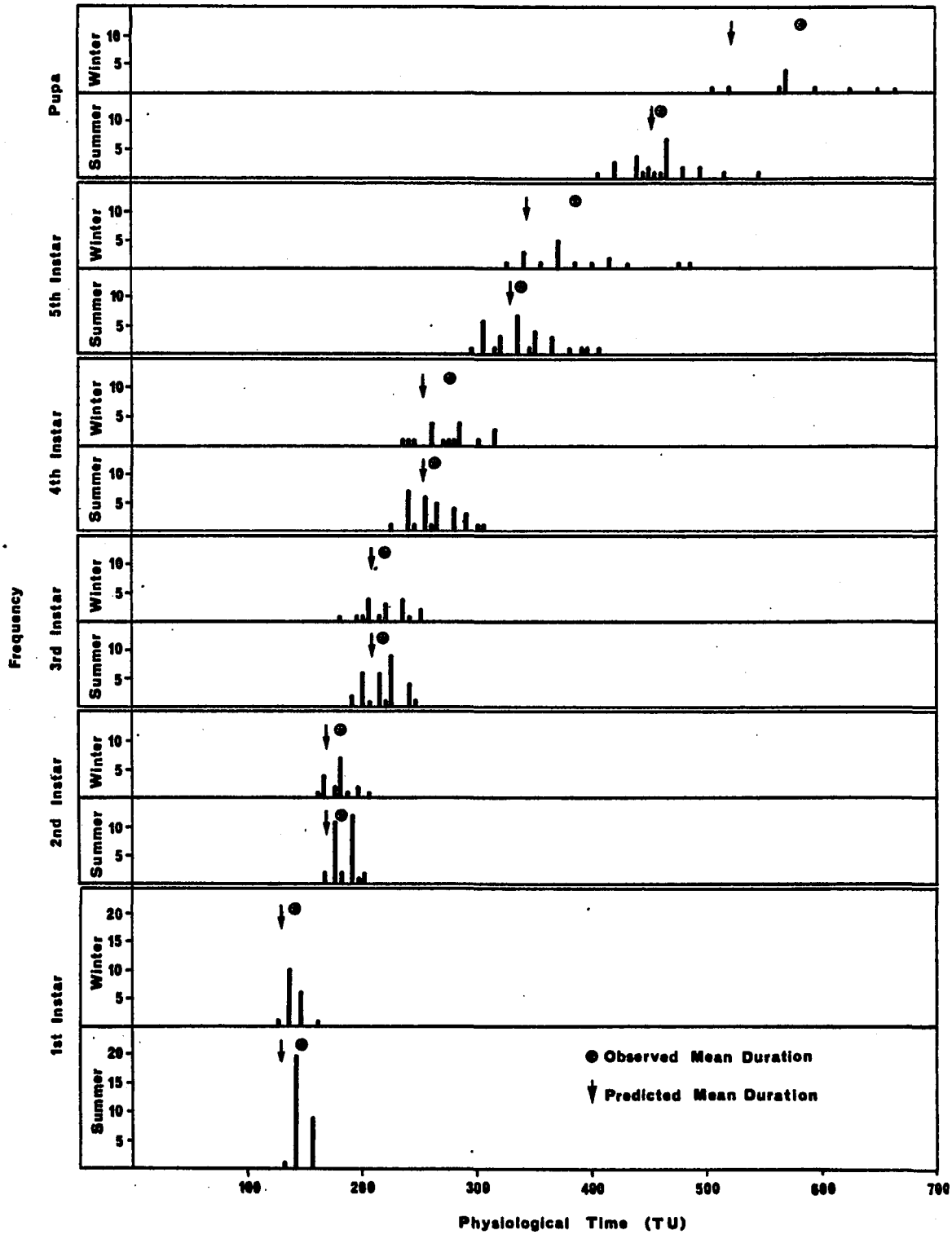
[c] Thermal units required for development in the greenhouse verification experiment.

Histograms of frequency distributions of the duration of life stages obtained in the greenhouse verification experiment and their relationship to the mean duration predicted by the fluctuating temperature model were drawn (Figure 18).

3. Field verification of thermal unit model

Based on the thermal unit model, adult emergence of the orange moth, developing through 5 larval stadia, should occur after the accumulation of 456.51 T.U.s. In order to validate that this model accurately predicted development in the field, the SI flight, monitored during 1976, 1977, and 1978, was evaluated. The theoretical biofix for the overwintering population was used as the starting point for thermal unit accumulations. The theoretical biofix, as defined in Section IV. A. 3, occurs when the photophase equals or exceeds 13 hours and the temperature at false dawn is $\geq$ 8.85°C. The photophase on April 7 equals 13 hours. If the temperature at false dawn and at dusk is $\geq$ 8.85°C, then the overwintering WIV generation will mate and oviposit SI eggs. The theoretical biofix for the WIV population occurred on April 7 (Julian Dt. 98) in 1976, on April 9 (Julian Dt. 99) in 1977, and on April 7 (Julian Dt. 97) in 1978. T.U.s were accumulated daily from the biofix date. Emergence of SI adults was predicted to occur on June 5 (Julian Dt. 157) in 1976, on May 23 (Julian Dt. 143) in 1977, and on June 8 (Julian Dt. 159) in 1978, 456.51 T.U.s after the theoretical biofix. SI adults were active on June 5 (Julian Dt. 157) in 1976, on May 23 (Julian Dt. 143) in 1977, and on June 8 (Julian Dt. 159) in 1978. Therefore, the thermal unit model, in combination with

Figure 18. Frequency histograms of the mean durations on a T.U. scale for immature stages of individuals (summer and winter color morph) reared in the greenhouse verification experiment


Pupa
5th Instar
4th Instar
3rd Instar
2nd Instar
1st Instar
Winter
Summer
Frequency
Observed Mean Duration
Predicted Mean Duration
Physiological Time (TU)
100
200
300
400
500
600
700

the theoretical biofix for the WIV overwintering generation, accurately predicted the occurrence of the SI flight. It is likely that the predicted date for SI emergence does not correspond to the beginning of the SI flight. Assuming that the theoretical biofix marks the beginning of the ovipositional period of the WIV generation, emergence of approximately 50% of the adults produced from the first ovipositional cohort should occur after the accumulation of 456.51 T.U.s. Because the predicted T.U. accumulation for emergence is a mean value, some moths will emerge prior to the predicted T.U. accumulation. Therefore, the predicted date for SI emergence probably corresponds to the first significant peak in moth emergence.

E. Color Morph Development

1. Interaction between photoperiod and instar

Acleris minuta adults exhibit dimorphic coloration, the summer adults (SI, SII, SIII) emerging as orange moths and the overwintering (WIV) adults emerging as gray moths. Because each dimorphic state is present during a specific time of year, the stimulus required to trigger the switch in color morph development is probably seasonal. Photoperiod is the most likely and consistent seasonal stimulus.

In the laboratory, larvae reared under a 12L/12D photoperiod regime consistently emerge as gray moths, while larvae reared under a 16L/8D photoperiod regime emerge as orange moths. A laboratory experiment was designed to determine the interaction between photoperiod and stage of development. Larvae from each larval stadium were taken from a simulated

summer photoperiod (16L at 27°C/8D at 16°C) and exposed to a simulated winter photoperiod (12L at 27°C/12D at 16°C). Individuals exposed to a winter photoperiod during the 1st, 2nd, or 3rd stadium and for the duration of their immature life emerged as gray moths (Table 38). Exposure to winter photoperiods during the 4th stadium resulted in the emergence of both color morphs (Table 38).

Based upon laboratory experiments, the critical duration of the photophase that triggers gray color morph development is between 12 and 16 hours. Apparently larvae are not committed to the gray developmental scheme until the 4th instar. Exposure to a critical photophase after the 4th instar will not produce a gray moth.

Dates associated with peak larval densities of all instars and the durations of the photophases occurring on these dates for all generations (1977, 1978) were listed (Table 39). Because intensive population sampling of the SI generation was not attempted, dates listed for the SI generation were calculated based upon the thermal unit model and the thermal units accumulated in 1978. The thermal unit model predicts that 4th instars of the SI generation should be present on May 23 (Julian Dt. 143). The peak population densities of 4th instars (based on field samples) for the SII, SIII, and WIV generations occurred on June 9 (Julian Dt. 160), July 15 (Julian Dt. 196), and August 18 (Julian Dt. 230) in 1977 and on June 26 (Julian Dt. 177), August 3 (Julian Dt. 215), and September 6 (Julian Dt. 249) in 1978, respectively. Photophases > 14 hours occurred during the 4th instar population peaks of the SI, SII, and SIII generations in 1977 and 1978. Photophases < 14 hours occurred during the 4th

Table 38. Frequencies of laboratory emerging moths belonging to each color morph scheme

Treatment[a] - Instar No.[b]	Summer Moths	Winter Moths
Winter - 1, 2, 3, 4, 5	0	7
Summer - 1; Winter - 2, 3, 4, 5	0	23
Summer - 1, 2; Winter - 3, 4, 5	1	5
Summer - 1, 2, 3; Winter - 4, 5	6	8
Summer - 1, 2, 3, 4; Winter - 5	10	0
Summer - 1, 2, 3, 4, 5	10	0

[a] Winter = simulated winter photoperiod (12L at 27°C/12D at 16°C), summer = simulated summer photoperiod (16L at 27°C/8D at 16°C).

[b] 1 = 1st instar, 2 = 2nd instar, 3 = 3rd instar, 4 = 4th instar, 5 = 5th instar.

Table 39. Dates of peak population densities for each developmental stage (1977, 1978) and associated photophases

Stage (Instar)		SI	SII		SIII		WIV	
		1978	1977	1978	1977	1978	1977	1978
1st	Dt.[a]	128		167	188	203	220	245
	Photo.[b]	13:57		15:14	15:07	14:46	14:10	13:09
2nd	Dt.	134		171	188	211	220	245
	Photo.	14:23		15:15	15:07	14:30	14:10	13:09
3rd	Dt.	139	153	171	188	211	230	245
	Photo	14:33	15:03	15:15	15:07	14:30	13:45	13:09
4th	Dt.	143	160	177	196	215	230	249
	Photo.	14:43	15:10	15:14	14:57	14:22	13:45	12:56
5th	Dt.	148	167	177	196	217	230	252
	Photo.	14:55	15:14	15:14	14:57	14:17	13:45	12:48
6th	Dt.	147	167	185	203	233	244	257
	Photo.	14:55	15:14	15:09	14:46	13:38	13:09	12:33
7th	Dt.	147	167	192	210	233	244	257
	Photo.	14:55	15:14	15:02	14:32	13:38	12:48	12:27

[a] Dt. = Julian Date.

[b] Photo. = photophase expressed as hours:minutes.

instar population peaks of the WIV generations (1977, 1978). Based upon these data, photophases > 14 hours may cause larvae to develop into orange moths, while photophases < 14 hours may cause larvae to develop into gray moths.

F. Life Tables

1. Experimental life tables

Experimental life tables were constructed for cohorts of individuals reared under 15°, 18°, 22°, and 24°C, mean fluctuating temperature. The net reproductive rate (R_o), the generation time (T_c), the capacity for increase (R_c), the instantaneous birth rate (B), the instantaneous death rate (D), the finite rate of increase (λ), and the stable age distribution for individuals developing under each rearing temperature were summarized (Table 40). These statistics were developed from data utilized in the construction of experimental life tables. The net reproductive rate, the number of times a population will multiply per generation, is 79.41, 75.11, 96.40, and 58.50 for the cohorts reared at 24°, 22°, 18°, and 15°C, respectively. This statistic indicates that the greatest increase in population occurred under the 18°C rearing condition. However, because of the extended generation time at 18°C the rate of increase at 18°C was less than the rate at 22° and at 24°C, but greater than the rate at 15°C. The generation time can be defined as the mean age, in days, of the females in the cohort at the birth of 50% of their daughters. The generation time for the cohorts reared at 15°C (74.37 days) was 33.83 days longer than the generation time for the cohorts reared at 24°C (40.54

Table 40. The net reproductive rate (R_o), the generation time (T_c), the capacity for increase (R_c), the instantaneous birth rate (B), the instantaneous death rate (D), the finite rate of increase (λ), and the stable age distribution for cohorts of laboratory reared individuals

Temperature	R_o	T_c	R_c	B	D	λ	Stable Age Dist.	
							Prerep.	Rep.
24°C	79.41	40.54	0.11	0.12	0.01	1.12	98.69	1.31
22°C	75.11	43.04	0.10	0.10	0.00	1.11	98.59	1.41
18°C	96.40	55.33	0.08	0.09	0.01	1.08	98.15	1.85
15°C	58.50	74.37	0.05	0.06	0.01	1.06	97.56	2.44

days). Unlike the net reproductive rate, the capacity for increase and the finite rate of increase incorporate the differences in generation times, resulting in statistics that can be compared between and within species. The capacity for increase describes "the growth potential per unit time of a population with a stable age distribution under given climatic and food conditions" (Andrewartha and Birch 1945). The capacity for increase equals 0.11, 0.10, 0.08, and 0.05 for cohorts reared at 24°, 22°, 18°, and 15°C, respectively.

As rearing conditions approach the tolerable limits of the species, the rate of population increase declines. R_c values < 0 indicate that the population is declining. Three factors causing decreases in the capacity for increase include: 1) increases in the death rate, 2) reduced fecundity, and 3) increases in the generation time. Under controlled rearing conditions within the tolerable range of the species, senility is the major mortality factor. The instantaneous death rates per unit time for the cohorts with stable age distributions were determined (Table 40). The resulting low instantaneous death rates indicate that mortality during the immature stages is minimal. Within the temperature ranges utilized in this experiment, fecundity (net reproductive rate) remained relatively stable. It would be expected that under more adverse conditions the declining nutritional state of the larvae and/or an increased death rate would reduce the realized fecundity significantly. The factor that most drastically reduced the capacity for increase was the delayed maturation period associated with increased generation time. Under the relationship

developed during this experiment, for each 10-day increase in generation time there would be a decrease of .02 in the capacity for increase.

2. Ecological life tables

Ecological life tables were constructed from field population studies for the SII, SIII, and WIV generations in 1977 and 1978 (Tables 41 - 46). Total egg to adult mortality equaled 85% for the SII generation (1977), 98% for the WIV generation (1977), 75% for the SII generation (1978), 86% for the SIII generation (1978), and 91% for the WIV generation (1978).

The net reproductive rate for the field population was well below the rate for the laboratory population (Table 47). The differences between the net reproductive rates and the approximate capacities for the 2 populations are because of environmental constraints upon the populations and sampling errors associated with field density estimates.

The only causal agents of mortality identified during the construction of the life tables were parasitoids. Thirty-two species of primary or secondary parasitoids were reared from the host, but only 10 caused consistent and significant mortality ($\geq$ 0.10%). The 10 most important parasitoids are those listed in the ecological life tables (Tables 41 - 46). In order to determine if any of the mortality factors identified in the ecological life tables were key factors, the "killing value" (k_i) for each mortality factor was regressed on the total generation mortality (K) for the 6 generations. The regressions for the 15 major mortality factors were determined (Table 48). Comparison of the regression coefficients indicates the relative importance of each submortality factor.

Table 41. Ecological life table for the second generation (1977)

Age interval (x)	No. alive per 100 trees (lx)	lx-dx	Factor responsible for dx (dxF)
Egg			
Instars 1, 2, 3	265		
			Apanteles sp.
		245.85	
			Other
Instars 4, 5, 6, 7	144		
			Temelucha forbesi
		133.64	
			Temelucha sp.
		130.32	
			Pristomerus austrinus
		126.90	
			Other
Pupae	87		
			Itoplectis conquisitor
		85.24	
			Chorinaeus excessorius
		83.48	
			Other
Adults	43		
			Sex ratio (51% females)
Females	22		
			Mating success (81%)
Fecund females	18		
			Fecundity (45% of 289.64)
Eggs (SIII)	2346		

No. dying during x (dx)	dx as a % of lx (100qx)	Log lx	k - value
		2.4232	
18.15	6.85		.0308
		2.3924	
102.85	38.81		.2340
		2.1584	
10.26	7.12		.0321
		2.1263	
3.42	2.38		.0113
		2.1150	
3.42	2.38		.0115
		2.1035	
39.90	27.71		.1640
		1.9306	
1.76	2.02		.0088
		1.9306	
1.76	2.02		.0090
		1.9216	
40.48	46.53		.2881
		1.6335	
21.00	49.00		
4.18	19.99		
2867.52	55.00		
		Total generation mortality (K)	.7896

Table 42. Ecological life table for the third generation (1977)

Age interval (x)	No. alive per 100 trees (lx)	lx-dx	Factor responsible for dx (dxF)
Egg	471		
Instars 1, 2, 3	520		
			Apanteles sp.
		518.74	
			Other
Instars 4, 5, 6, 7	457		
			Temelucha sp.
		453.78	
			Other
Pupae	135		
			Itoplectis conquisitor
		133.02	
			Nemorilla pyste
		132.36	
			Other
Adults	69		
			Sex ratio (50% females)
Females	34		
			Mating success (81%)
Fecund females	28		
			Fecundity (45% of 289.64)
Eggs (WIV)	3649		

No. dying during x (dx)	dx as a % of lx (100qx)	Log lx	k - value
		2.7160	
1.26	0.24		.0011
		2.7149	
61.74	11.87		.0550
		2.6599	
3.22	0.70		.0031
		2.6568	
318.78	69.75		.5265
		2.1303	
1.98	1.47		.0064
		2.1239	
.66	0.49		.0021
		2.1218	
63.36	46.93		.2830
		1.8388	
34.50	50.00		
6.00	19.00		
4460.92	55.00		
		Total generation mortality (K)	.8772

Table 43. Ecological life table for the fourth generation (1977)

Age interval (x)	No. alive per 100 trees (lx)	lx-dx	Factor responsible for dx (dxF)
Eggs	1399		
			Trichogramma sp.
		699.50	
			Other
Instars 1, 2, 3	454		
			Apanteles sp.
		447.77	
			Other
Instars 4, 5, 6, 7	365		
			Oncophanes americanus
		362.07	
			Other
Pupae	72		
			Itoplectis conquisitor
		58.40	
			Chorinaeus excessorius
		57.60	
			Other
Adults	32		
			Sex ratio (30% females)
Females	10		

No. dying during x (dx)	dx as a % of lx (100qx)	Log lx	k - value
		3.1458	
699.50	50.50		.3010
		2.8448	
245.50	18.00		.1877
		2.6571	
6.23	1.37		.0060
		2.6511	
82.77	18.23		.0888
		2.5623	
2.93	0.80		.0035
		2.5588	
290.07	79.47		.7015
		1.8573	
13.60	18.89		.0909
		1.7664	
0.80	1.11		.0060
		1.7604	
25.60	35.56		.2553
		1.5051	
22.4	70.00		

Total generation mortality (K)	1.6407

Table 44. Ecological life table for the second generation (1978)

Age interval (x)	No. alive per 100 trees (lx)	lx-dx	Factor responsible for dx (dxF)
Egg	106		
			Trichogramma sp.
		102.60	
			Other
Instars 1, 2, 3	72		
Instars 4, 5, 6, 7	77		
			Oncophanes americanus
		74.90	
			Other
Pupae	35		
			Brachymeria ovata
		34.28	
			Spilochalis sp.
		33.96	
			Chorinaeus excessorius
		33.88	
			Itoplectis conquisitor
		33.83	
			Hyperparasites
		33.35	
			Other
Adults	27		
			Sex ratio (52% of females)
Females	14		
			Mating success (81%)
Fecund Females	11		
			Fecundity (45% of 289.64)
Eggs (SIII)	1434		

No. dying during x (dx)	dx as a % of lx (100qx)	Log lx	k - value
		2.0253	
3.40	3.0		.0142
		2.0111	
30.60	29.0		.1538
		1.8573	
		1.8865	
2.10	3.0		.0120
		1.8745	
39.90	52.0		.3304
		1.5441	
0.72	2.0		.0091
		1.5350	
0.32	0.9		.0040
		1.5310	
0.08	0.2		.0011
		1.5299	
0.05	0.1		.0006
		1.5293	
0.48	1.0		.0062
		1.5231	
6.35	18.0		.0917
		1.4314	
12.96	48.0		
2.66	19.0		
1752.32	55.0		
		Total generation mortality (K)	.5939

Table 45. Ecological life table for the third generation (1978)

Age interval (x)	No. alive per 100 trees (lx)	lx-dx	Factor responsible for dx (dxF)
Egg	199		
			Trichogramma sp.
		192.70	
			Other
Instars 1, 2, 3	157		
			Apanteles sp.
		148.59	
			Other
Instars 4, 5, 6, 7	128		
			Oncophanes americanus
		125.78	
			Sinophous sp.
		125.04	
			Temelucha sp.
		124.60	
			Pristomerus austrinus
		123.12	
			Hyperparasites
		117.94	
			Other
Pupae	54		
			Brachymeria ovata
		51.84	
			Spilochalis sp.
		51.57	
			Chorinaeus excessorius
		51.43	
			Hyperparasites
		49.27	
			Other
Adults	27		
			Sex ratio (48% females)
Females	13		
			Mating success (81%)
Fecund Females	10		
			Fecundity (51% of 289.64)
Eggs (WIV)	1477		

No. dying during x (dx)	dx as a % of lx (100qx)	Log lx	k - value
		2.2989	
6.30	3.00		.0140
		2.2849	
35.70	18.00		.0890
		2.1959	
8.41	5.00		.0239
		2.1720	
20.59	13.00		.0648
		2.1072	
2.22	2.00		.0076
		2.0996	
0.74	0.50		.0026
		2.0970	
0.44	0.30		.0015
		2.0955	
1.48	1.00		.0052
		2.0903	
5.18	4.00		.0186
		2.0717	
63.94	50.00		.3393
		1.7324	
2.16	5.00		.0177
		1.7147	
0.27	0.50		.0023
		1.7124	
0.14	0.25		.0012
		1.7112	
2.16	4.00		.0186
		1.6926	
22.27	41.00		.2612
		1.4314	
14.04	52.00		
2.47	19.00		
1419.24	49.00		
		Total generation mortality (K)	.8675

Table 46. Ecological life table for the fourth generation (1978)

Age interval (x)	No. alive per 100 trees (lx)	lx-dx	Factor responsible for dx (dxF)
Egg	174		
			Trichogramma sp.
		147.76	
			Other
Instars 1, 2, 3	110		
			Apanteles sp.
		105.38	
			Other
Instars 4, 5, 6, 7	96		
			Oncophanes americanus
		93.08	
			Sinophous sp.
		92.64	
			Temelucha sp.
		91.18	
			Hyperparasites
		82.42	
			Other
Pupae	23		
			Brachymeria ovata
		22.79	
			Spilochalis sp.
		22.72	
			Chorinaeus excessorius
		21.67	
			Itoplectis conquisitor
		21.18	
			Hyperparasites
		20.02	
			Other
Adults	16		
			Sex ratio (38% females)
Females	6		

No. dying during x (dx)	dx as a % of lx (100qx)	Log lx	k - value
		2.2405	
26.24	15.00		.0709
		2.1696	
37.76	22.00		.1282
		2.0414	
4.62	4.00		.0186
		2.0228	
9.38	9.00		.0405
		1.9823	
2.92	3.00		.0134
		1.9689	
0.44	0.40		.0021
		1.9668	
1.46	2.00		.0069
		1.9599	
8.76	9.00		.0439
		1.9160	
59.42	62.00		.5543
		1.3617	
0.21	0.90		.0040
0.07	0.30		.0013
		1.3564	
1.05	5.00		.0205
		1.3359	
0.49	2.00		.0100
		1.3259	
1.16	5.00		.0244
		1.3015	
4.02	17.00		.0974
		1.2041	
10.00	63.00		
	Total generation mortality (K)		1.0364

Table 47. The net reproductive rate (R_o) and the approximate capacity for increase (R_c) as determined from life table analyses of field and laboratory populations

Population	R_o	R_c
Field		
SIII (1977)	2.97	0.03
SII (1978)	1.88	0.02
SIII (1978)	0.87	-0.003
Laboratory	58.50 - 96.40	0.05 - 0.11

Table 48. Regression of submortality factors (k_{1-15}) on total generation mortality (K)

Life Stage	Mortality Factor	Regression	R^2
Egg	*Trichogramma* sp. (k_1)	$k_1 = -.2053 + .2951$ (K)	.93
	other (k_2)	$k_2 = .0847 + .0531$ (K)	.32
Instars 1, 2, 3	*Apanteles* sp. (k_3)	$k_3 = .0349 + -.0181$ (K)	.26
	other (k_4)	$k_4 = .1545 + -.0555$ (K)	.06
Instars 4, 5, 6, 7	*O. americanus* (k_5)	$k_5 = .0169 + -.0075$ (K)	.55
	Temelucha sp. (k_6)	$k_6 = .0067 + -.0030$ (K)	.06
	P. austrinus (k_7)	$k_7 = .0066 + -.0040$ (K)	.09
	Sinophorus sp. (k_8)	$k_8 = .0010 + -.0002$ (K)	.00
	other (k_9)	$k_9 = .0231 + .4267$ (K)	.63
Pupa	*I. conquisitor* (k_{10})	$k_{10} = -.0695 + .0919$ (K)	.88
	C. excessorius (k_{11})	$k_{11} = .0013 + .0051$ (K)	.06
	B. ovata (k_{12})	$k_{12} = .0125 + -.0076$ (K)	.15
	Spilochalis sp. (k_{13})	$k_{13} = .0037 + -.0025$ (K)	.31
	Hyperparasites (k_{14})	$k_{14} = .0119 + -.0039$ (K)	.02
	other (k_{15})	$k_{15} = .1510 + .0638$ (K)	.06

The mortality factor acting on larval instars 4, 5, 6, and 7 identified as "other (k_9)" is the key factor. The "other" mortality factor was calculated by subtracting the mortality due to parasitoids from the total larval mortality. Therefore, this mortality factor includes losses of larvae due to migration, predation, disease and unknown causes.

The relationship between each k_i value and the population density of the stage on which it acted was investigated by regressing the k_i value on the log of the population density (Table 49). Regressions of density dependent mortality factors, factors that have an increasingly adverse effect as the population density increases, have a positive slope and a large R^2 value indicating that the regression is a good fit. Regressions with a negative slope indicate inverse density dependence and regressions with a slope equal to zero indicate density independence. Based upon this regression technique, the mortality caused by the egg parasitoid, Trichogramma sp., is density dependent. However, it should be emphasized that the 2 variables, the k value and the log of the population density, are not independent and the relationship determined by the regression technique may be a result of sampling error. The regression coefficient (.2676) indicates that this factor will not be able to compensate for population increases and its role in equilibrium maintenance is limited. Based upon the data compiled during 1977 and 1978, the only other factor that may demonstrate density dependence is the "other" mortality factor (k_{15}) for the pupal stage. Additional research is needed to clarify the mortality factors included in the "other" classi-

Table 49. Regression of submortality factors (k_{1-15}) on population density log(N)

Life Stage	Mortality Factor	Regression	R^2
Egg	*Trichogramma* sp. (k_1)	$k_1 = -.5503 + .2676 \log(N)$	.93
	other (k_2)	$k_2 = .0144 + .0515 \log(N)$	.37
Instars 1, 2, 3	*Apanteles* sp. (k_3)	$k_3 = .0837 + -.0281 \log(N)$	.44
	other (k_4)	$k_4 = -.0033 + .0415 \log(N)$	.02
Instars 4, 5, 6, 7	*O. americanus* (k_5)	$k_5 = .0381 + -.0144 \log(N)$	.59
	Temelucha sp. (k_6)	$k_6 = .0096 + -.0026 \log(N)$	.03
	P. austrinus (k_7)	$k_7 = .0090 + -.0028 \log(N)$	.03
	Sinophorus sp. (k_8)	$k_8 = .0045 + -.0017 \log(N)$	.18
	other (k_9)	$k_9 = -.3053 + .3329 \log(N)$	.29
Pupa	*I. conquisitor* (k_{10})	$k_{10} = -.0209 + .0229 \log(N)$	.03
	C. excessorius (k_{11})	$k_{11} = .0346 + -.0161 \log(N)$	.33
	B. ovata (k_{12})	$k_{12} = .0239 + -.0106 \log(N)$	.17
	Spilochalis sp. (k_{13})	$k_{13} = .0079 + -.0038 \log(N)$	.42
	Hyperparasites (k_{14})	$k_{14} = .0611 + -.0301 \log(N)$	.61
	other (k_{15})	$k_{15} = -.3086 + .2963 \log(N)$	.80

fications. Density dependent factors and density independent factors probably are concealed within this classification.

Due to the problems associated with the regression technique and the limited range of A. minuta population densities during 1977 and 1978, caution should be exercised in classifying any of the factors as density dependent or density independent.

V. SUMMARY

A. Introduction

A schematic diagram of the life system of A. minuta (Figure 1) was presented in Section I. This summary extracts from Section IV the quantifiable relationships utilized in the construction of the conceptual model of the life system.

The conceptual model of the life system of A. minuta can be divided into 4 major subsystems.

Subsystem I - Fecundity and Oviposition

Subsystem II - Development of Larval Instars 1 - 4

Subsystem III - Development of Larval Instars 5, 6, and 7 Under a Summer or Winter Color Morph Scheme

Subsystem IV - Overwintering

Simulation begins with the input of pupae into Subsystem I. The population dynamics for each generation are simulated and a daily estimate of the density of each life stage is printed.

Each concept and each relationship utilized in the conceptual model are referenced to the particular subsection, where the topic was presented originally, by an internal reference system. The symbols contained within the brackets, that follow each concept or relationship, correspond to the subsection numbers listed in the Table of Contents. That is, "a theoretical biofix [IV. A. 3] will be established for the overwintering adult population." An explanation of the theoretical biofix concept can be found in Subsection IV. A. 3 of the Results and Discussion section

entitled "Temporal relationships between adult flights and population phenology" found on page 64. The remaining subsections of the Summary are devoted to the development of the 4 subsystems.

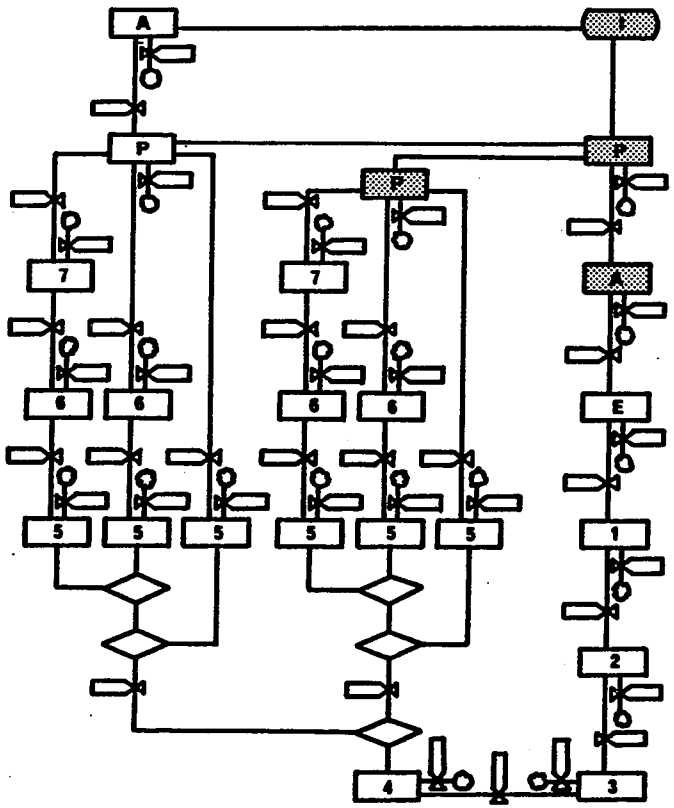
B. Fecundity and Ovipositional Subsystem (Subsystem I)

The fecundity and ovipositional subsystem (Figures 19 & 20) predicts numerical values for the state variables, i.e., population densities, for 3 components: 1) pupae, 2) moths, and 3) eggs. Population densities for these 3 components are simulated daily. There are two routes of entry into this subsystem. Pupae may enter this subsystem as new entries or as outputs from Subsystem III (Figure 22).

A theoretical biofix [IV. A. 3] is established for the overwintering (WIV) adult population. In the spring when the photophase $\geq$ 13 hours [IV. A. 3] and the temperature at false dawn is $\geq$ 8.85°C [IV. B. 1], gray moths begin mating. The theoretical biofix indicates the beginning of the WIV ovipositional period [IV. A. 3]. If ovipositional period temperatures are $\geq$ 8.85°C, oviposition of SI eggs occurs [IV. B. 3]. The rate of physiological development of the life stages is determined based upon daily thermal unit accumulations. Thermal units for each day are calculated as the mean of the maximum and minimum temperatures (°C) minus the threshold temperature for development (8.85°C) [IV. D. 1]. If the minimum temperature is $<$ 8.85°C, then the minimum temperature is set equal to the developmental threshold, 8.85°C. Beginning at the WIV biofix, thermal units are accumulated and pupation for the SI generation occurs in the field after the accumulation of 331.95 T.U.s [IV. D. 1]. A

Figure 19. Schematic diagram of the fecundity and ovipositional subsystem and its relationship to the total life system: (A.) Total life system; (B.) fecundity and ovipositional subsystem. (Shaded components within the total life system diagram are the state variables included in the fecundity and ovipositional subsystem)

A.


A
P
7
6
5
4
3
2
1
E

B.

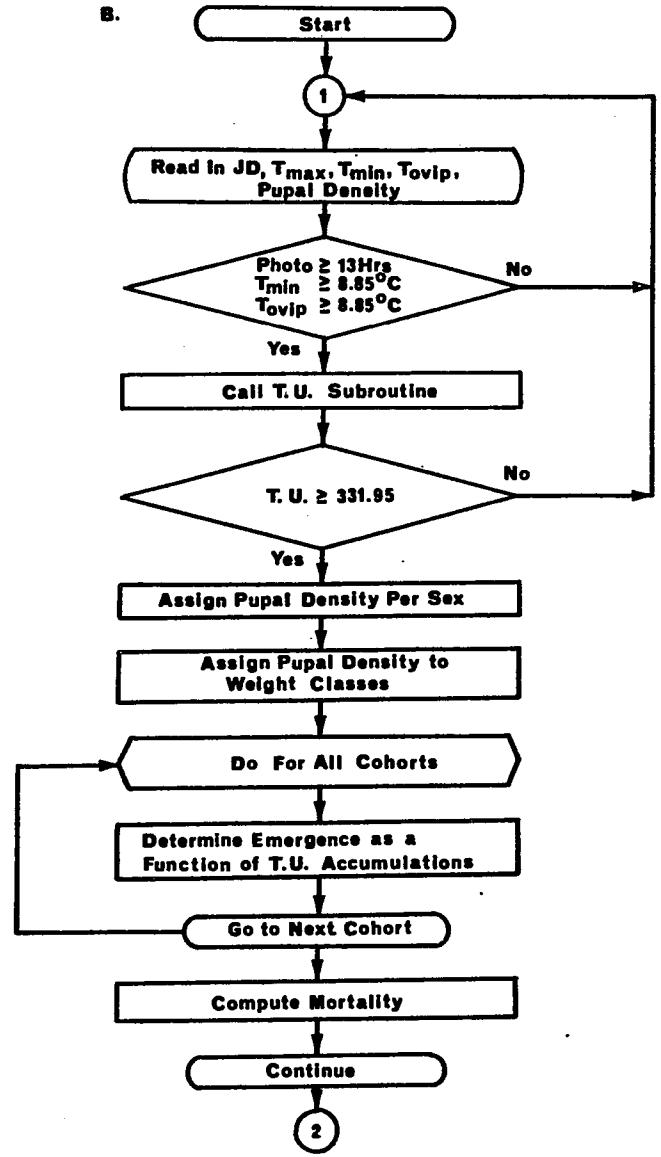
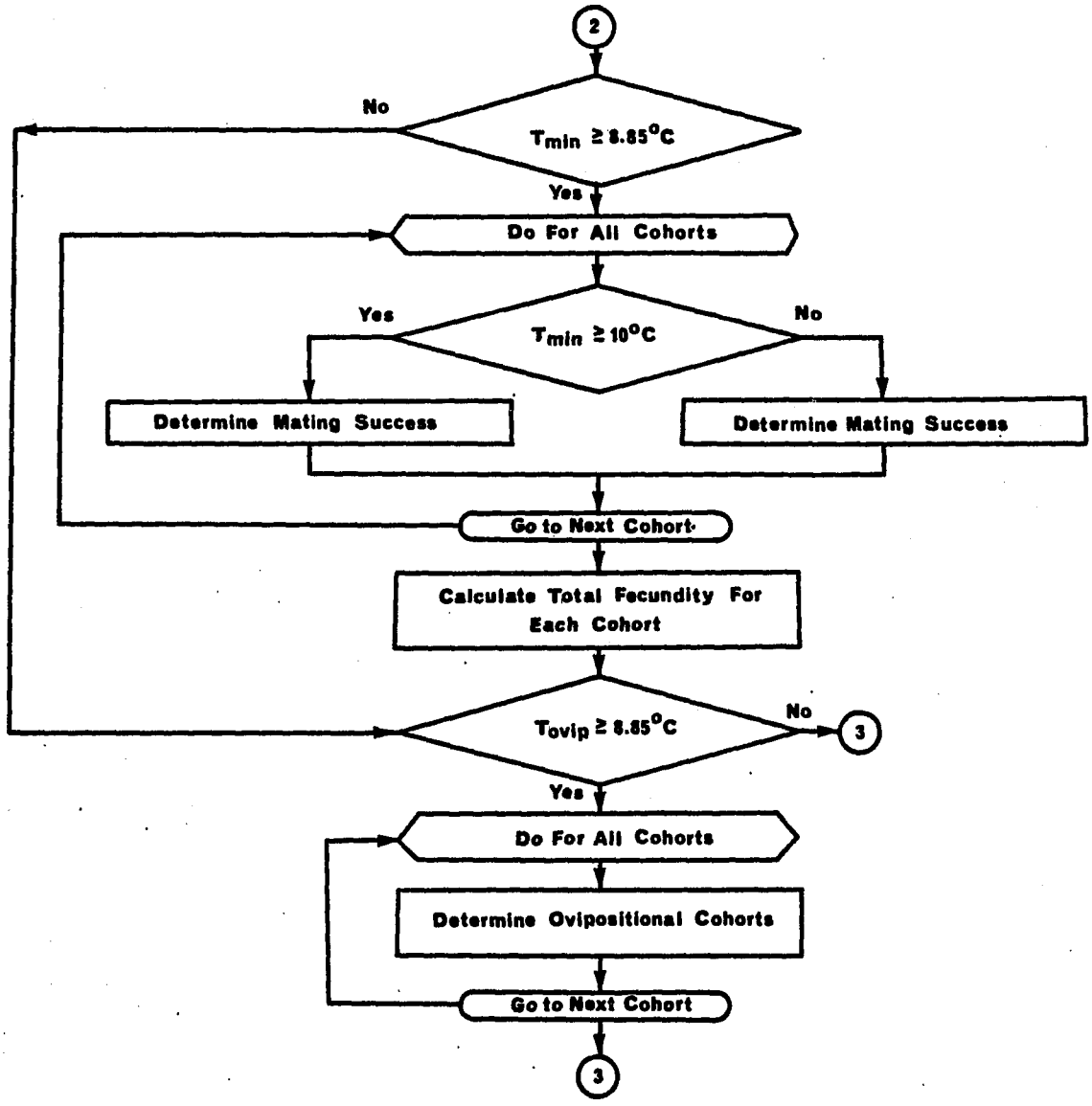

Start
1
Read in JD, Tmax, Tmin, Tovip, Pupal Density
Photo ≥ 13Hrs
Tmin ≥ 8.85°C
Tovip ≥ 8.85°C
No
Yes
Call T.U. Subroutine
T. U. ≥ 331.95
No
Yes
Assign Pupal Density Per Sex
Assign Pupal Density to Weight Classes
Do For All Cohorts
Determine Emergence as a Function of T.U. Accumulations
Go to Next Cohort
Compute Mortality
Continue
2

Figure 20. Continuation of the schematic diagram of the fecundity and ovipositional subsystem


2
No
$T_{min} \geq 8.85^{o}C$
Yes
Do For All Cohorts
Yes
$T_{min} \geq 10^{o}C$
No
Determine Mating Success
Determine Mating Success
Go to Next Cohort
Calculate Total Fecundity For Each Cohort
$T_{ovip} \geq 8.85^{o}C$
No
3
Yes
Do For All Cohorts
Determine Ovipositional Cohorts
Go to Next Cohort
3

field pupal sample (SI) is taken to initiate the pupal density (pupae/100 trees).

Analysis of the pupal mortality factors associated with the SII, SIII, and WIV generations indicates that none of the observed mortality is strongly density dependent and the combined mortality caused by all biotic and abiotic factors shows little linear relationship to pupal density. Life table analyses of the SII, SIII, and WIV generations reveal that a mean of 43% of the pupal population dies [IV. F. 2]. Therefore, 43% of the pupae are removed from the population. Female pupae weighing less than 16.00 mg and male pupae weighing less than 15.00 mg are eliminated first and the remaining proportion of the pupal mortality is selected from the remaining population in each weight class.

Pupae assigned to each weight class emerge at a rate determined by the probability density function of percentage emergence as a function of physiological time (T.U.s) [IV. D. 1]. The proportion of the summer females emerging on any particular day multiplied by the proportion of the female population in each weight class determines the number of females selected in each weight class to emerge during the daily thermal unit interval.

The daily cohort of emerging females in each weight class is given the opportunity to mate. Daily field conditions during the mating activity period, false dawn, determine the mating success rate [IV. B. 1]. If false dawn temperatures are $< 8.85°C$, mating does not occur. Days with false dawn temperatures $< 8.85°C$ are not counted and the 1-day old female cohort is added to the newly emerging cohort. If the temperature at false

dawn is ≥ 8.85°C but < 10°C, 73% of the daily cohort will mate during the next 4 days. The daily mating success rates of the female cohorts in each weight class on days 1, 2, 3, and 4, post emergence, average 13, 40, 13, and 7%, respectively [IV. B. 1]. If the temperature at false dawn is ≥ 10°C, 83% of the daily cohort will mate during the next 4 days. The daily mating success rates of these females in each weight class on days 1, 2, 3, and 4, post emergence, average 69, 0, 5, and 9%, respectively [IV. B. 1]. After 4 days, the unmated proportion of the female cohorts are considered non-competitive, and these individuals are removed from the system.

The total fecundity for the successfully mated female cohort is calculated by 1) multiplying the weight class density by the fecundity per female determined from the equation, $Y = -212.42 + 26.92 (X)$ where Y = fecundity per female and X = pupal weight in mg, and 2) summing the total fecundity for all weight classes [IV. B. 2].

The threshold temperature for oviposition closely parallels the threshold temperature for mating and development. If the temperature is ≥ 8.85°C during the ovipositional period, oviposition is behaviorally possible [IV. B. 3]. The mated cohorts oviposit a proportion of the total fecundity each day during the ovipositional period. The daily ovipositional proportion is calculated as the cumulative percentage oviposition predicted for day x + 1 minus the cumulative percentage oviposition predicted for day x. These cumulative percentages of the total fecundity are determined from the equation, $Y = -.56 + .30 \ln (X)$ where Y = cumulative percentage oviposition and X = T.U.s accumulated daily post mating [IV. B.

3]. The adult cohort will continue ovipositing daily egg cohorts until the T.U. accumulations (67 T.U.s) predict that 70% of the total fecundity has been oviposited. Environmental constraints prevent the oviposition of 100% of the total fecundity. The cohorts of eggs simulated daily enter Subsystem II (Figure 21).

C. Developmental Subsystem for Larval Instar 1 - 4 (Subsystem II)

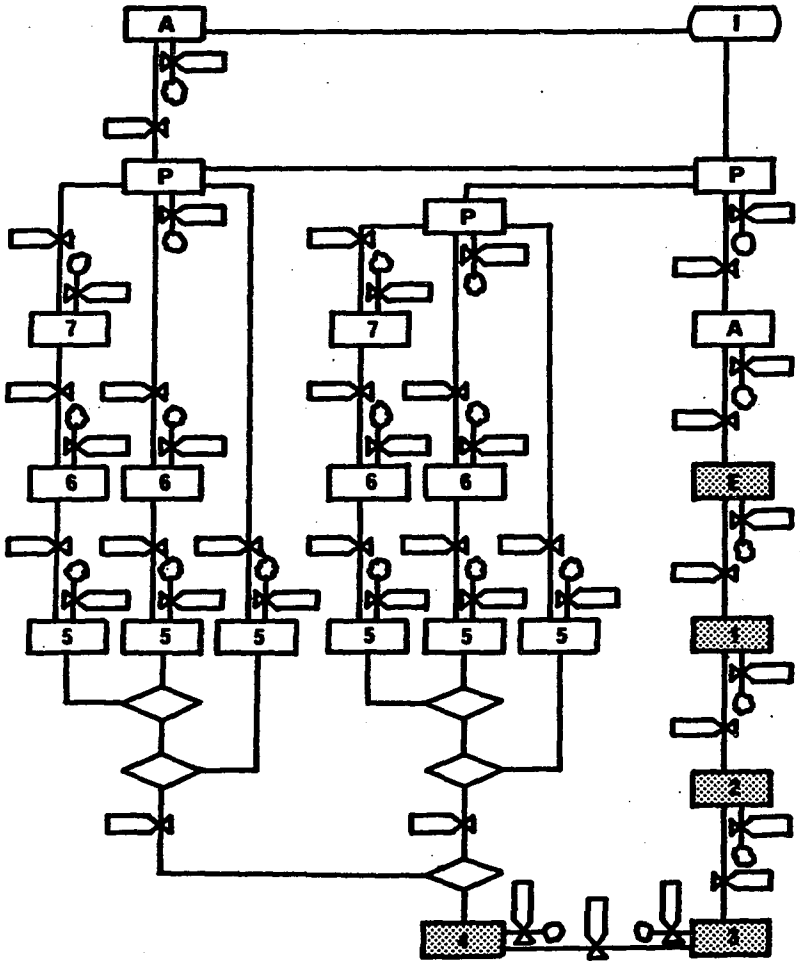
Each day a new cohort of eggs enters the Developmental Subsystem for Larval Instar 1 - 4 (Figure 21). This subsystem predicts numerical values for the state variables, i.e., population densities for 4 components: 1) 1st instars, 2) 2nd instars, 3) 3rd instars, and 4) 4th instars. Population densities for these components are simulated daily.

The proportion of the daily egg cohort that hatches is determined by the probability density function of percentage hatch as a function of physiological time (T.U.s) [IV. D. 1]. Egg mortality is simulated to coincide with eclosion. Egg mortality caused by Trichogramma sp. is density dependent and the proportion of the population that dies can be explained by the function $Y = -0.5503 + 0.2676 \log (X)$ where $Y = \log$ (total egg density/eggs alive after mortality) and X = total egg density [IV. F. 2]. Mortality due to Trichogramma sp. is calculated based on the egg density of each eclosing cohort. Additional egg mortality is constant (22%) and is removed from each cohort at eclosion [IV. F. 2].

Each day the proportion of the molting 1st instars is predicted using the probability density function of the percentage molting as a function of physiological time (T.U.s) [IV. D. 1]. Mortality is considered a

Figure 21. Schematic diagram of the developmental subsystem for larval instars 1-4 and its relationship to the total life system diagram: (A.) Total life system; (B.) developmental subsystem for larval instars 1-4. (Shaded components within the total life system diagram are the state variables included in the developmental subsystem for larval instars 1-4)

A.


A
I
P
P
P
7
7
A
6
6
6
6
E
5
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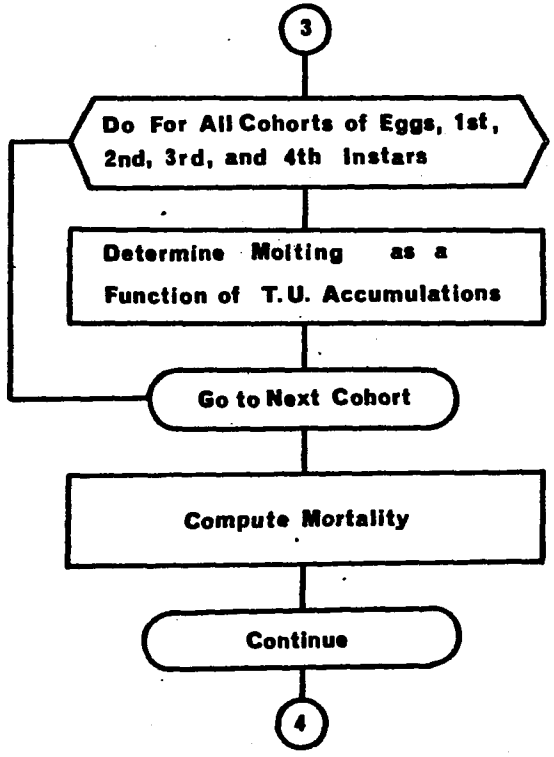
5
5
5
5
4
3
2
1
1

B.


3
Do For All Cohorts of Eggs, 1st, 2nd, 3rd, and 4th Instars
Determine Molting as a Function of T.U. Accumulations
Go to Next Cohort
Compute Mortality
Continue
4

constant resulting in the removal of 7% of each daily cohort at ecdysis [IV. F. 2].

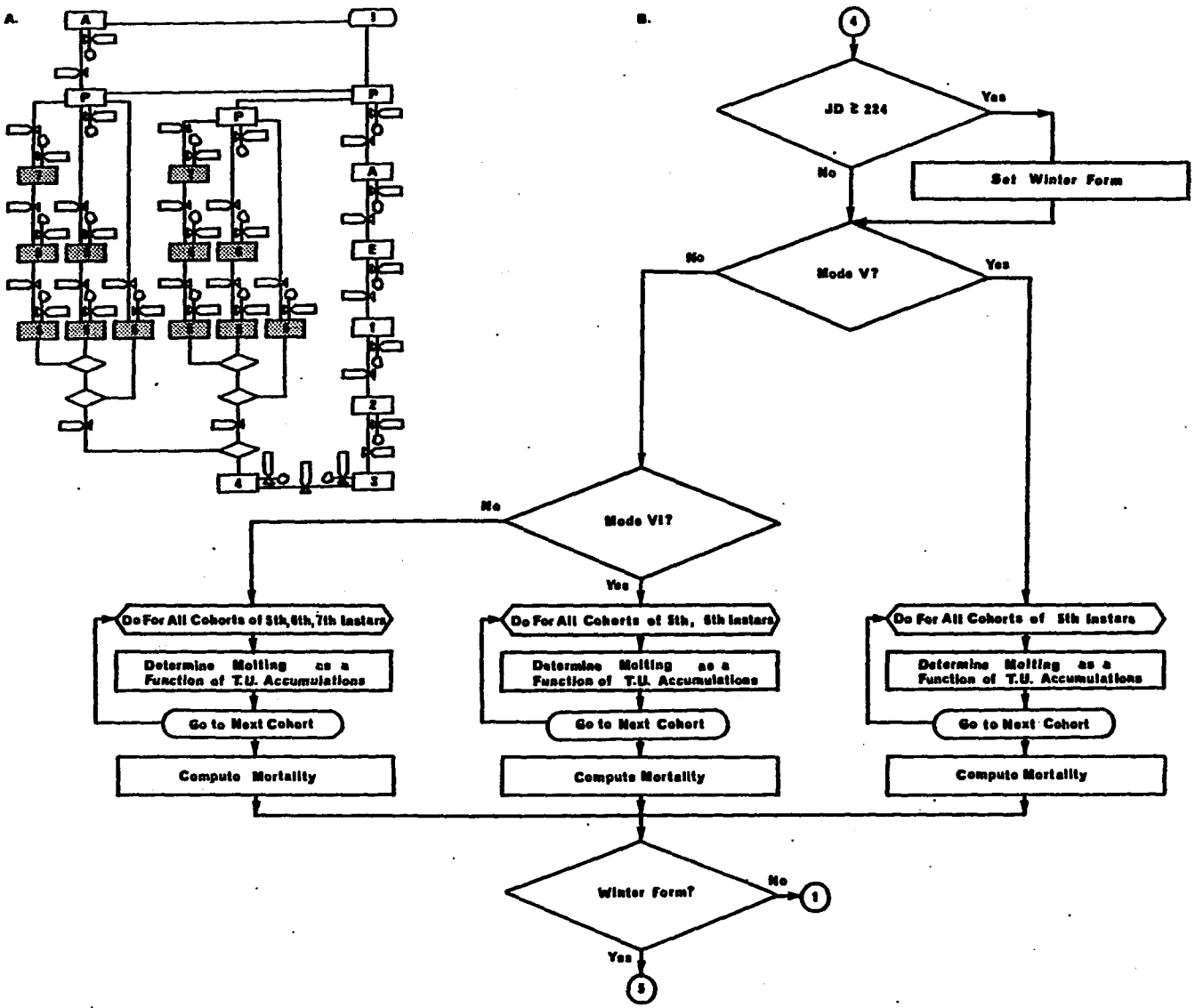
Similar loops are constructed for instars 2 & 3. During the 2nd instar loop, molting is predicted by the 2nd instar probability density function of the percentage molting as a function of physiological time (T.U.s) [IV. D. 1]. During the 3rd instar loop, molting is predicted by the 3rd instar probability density function. Mortality of both 2nd and 3rd instars is constant, and 7% of each daily cohort of both 2nd and 3rd instars are removed at ecdysis [IV. F. 2]. The cohorts of 4th instars simulated daily enter Subsystem III (Figure 22).

D. Developmental Subsystem for Larval Instars 5, 6, and 7 (Subsystem III)

Each day a new cohort of 4th instars enters the Developmental Subsystem for Larval Instars 5, 6, and 7 (Figure 22). This subsystem predicts numerical values for the state variables, i.e., population densities, for 6 components: 1) 5th instars (summer), 2) 5th instars (winter), 3) 6th instars (summer), 4) 6th instars (winter), 5) 7th instars (summer), and 6) 7th instars (winter). Population densities for these 6 components are simulated daily.

Daily cohorts of 4th instars entering Subsystem III encounter a Julian Date marker. If the Julian Date > 224, the daily cohort of 4th instars follows a gray development scheme. Julian Date is used to flag the date when the photophase decreases to < 14 hours of light [IV. E. 1]. Each day the proportion of the molting 4th instars within each color morph scheme is predicted using the summer or the winter probability density

Figure 22. Schematic diagram of the developmental subsystem for larval instars 5, 6, and 7 and its relationship to the total life system diagram: (A.) Total life system; (B.) developmental subsystem for larval instars 5, 6, and 7. (Shaded components within the total life system diagram are the state variables included in the developmental subsystem for larval instars 5, 6, and 7)


A.
B.
JD ≥ 224
Yes
No
Set Winter Form
Mode V?
No
Yes
Mode VI?
No
Yes
Do For All Cohorts of 5th,6th,7th Instars
Determine Molting as a Function of T.U. Accumulations
Go to Next Cohort
Compute Mortality
Do For All Cohorts of 5th, 6th Instars
Determine Molting as a Function of T.U. Accumulations
Go to Next Cohort
Compute Mortality
Do For All Cohorts of 5th Instars
Determine Molting as a Function of T.U. Accumulations
Go to Next Cohort
Compute Mortality
Winter Form?
No
Yes

function of the percentage molting as a function of physiological time (T.U.s) [IV. D. 1]. A constant mortality factor (16%) is removed, at ecdysis from each daily cohort of summer and winter 4th instars [IV. F. 2]. All daily cohorts of 4th instars pass through either the 4th instar summer or winter loop.

Daily cohorts of surviving 5th instars leave the 4th instar loop. After ecdysis, a determination is made of the proportion of the population that follows the 5 instar mode of development. The proportion of the population pupating after 5 stadia is determined by the probability density function of the proportion of the population assuming the 5 instar mode of development as a function of the nutritional value of the host plant [IV. C. 4]. As the seasonal nitrogen content of the leaves decrease and water stress increases, larval growth rates decline and greater proportions of the population go through supernumerary molts. The proportion of each daily cohort assigned to Mode V pupates at a rate determined by the probability density function of the percentage pupating as a function of physiological time (T.U.s) [IV. D. 1]. A constant mortality factor (16%) is removed at ecdysis [IV. F. 2]. The proportion of the population designated to pupate after more than 5 larval stadia is assigned to either the 6 instar mode or the 7 instar mode according to the probability density function of the percentage pupating after the 6th stadium as a function of the nutritional value of the host plant [IV. C. 4]. Each day the proportion of the 5th instars (Mode VI) molting to 6th instars is predicted using the probability density function of the

percentage molting as a function of physiological time (T.U.s) [IV. D. 1]. Likewise, the proportion of the 5th instars (Mode VII) molting to 6th instars is predicted using the probability density function for Mode VII development. Mortality is constant, removing 16% of each daily cohort of 5th instars (Mode VI) and 5th instars (Mode VII) [IV. F. 2]. All daily cohorts of 5th instars pass through 1 of 3 developmental mode sub-loops within either the summer or winter color morph scheme.

Similar loops are constructed for 6th instars, Mode VI and Mode VII, and 7th instars, Mode VII. Probability density functions for designated instars and modes of development predict the percentage of population pupating or molting as a function of physiological time (T.U.s) [IV. D. 1]. A 16% mortality factor is removed from all cohorts at either pupation or ecdysis [IV. F. 2].

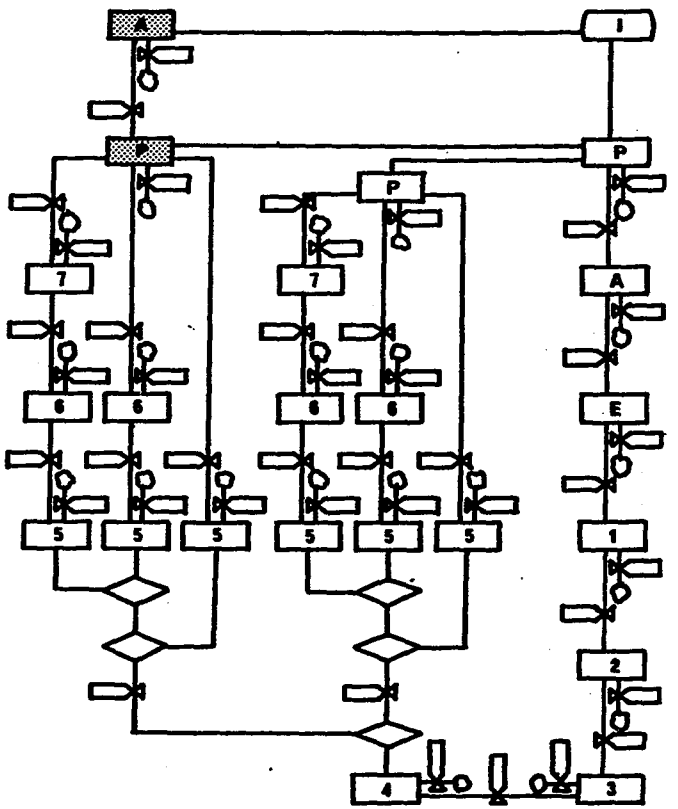
Daily cohorts of surviving pupae (summer color morph) of each of the developmental sub-loops leave Subsystem III (Figure 22) and enter Subsystem I (Figure 19 & 20). Daily cohorts of surviving pupae (winter color morph) leave Subsystem III (Figure 22) and proceed to Subsystem IV (Figure 23).

E. Overwintering Subsystem (Subsystem IV)

Each day a new cohort of pupae (winter color morph) enters the Overwintering Subsystem (Figure 23) from Subsystem III (Figure 22). This subsystem predicts numerical values for the state variables, i.e., population densities, for 4 components: 1) newly emerging males, 2) newly

Figure 23. Schematic diagram of the overwintering subsystem and its relationship to the total life system diagram: (A.) Total life system; (B.) overwintering subsystem. (Shaded components within the life system diagram are the state variables included in the overwintering subsystem)

A.


A
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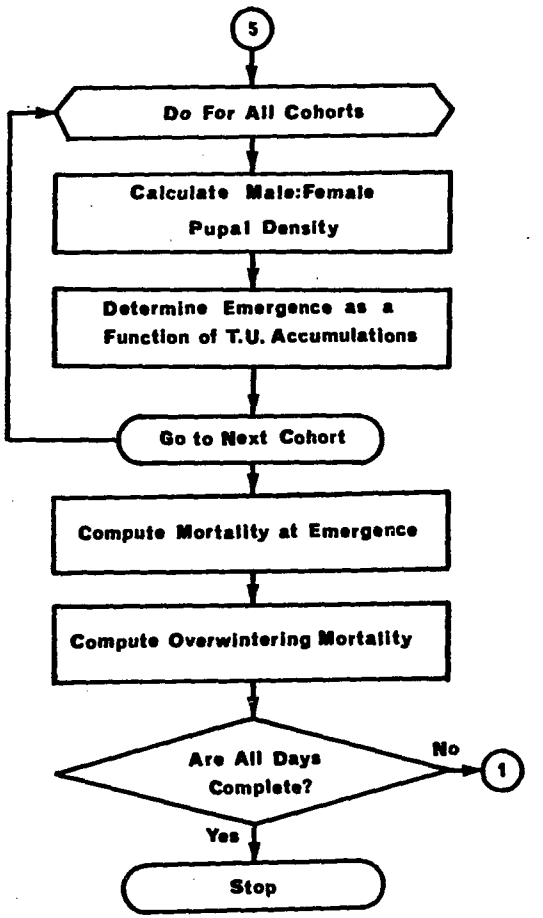
3

B.


5
Do For All Cohorts
Calculate Male:Female Pupal Density
Determine Emergence as a Function of T.U. Accumulations
Go to Next Cohort
Compute Mortality at Emergence
Compute Overwintering Mortality
Are All Days Complete?
No
1
Yes
Stop

emerging females, 3) successfully overwintered males, and 4) successfully overwintered females.

Assuming that the WIV pupal population has a 2:1 sex ratio (male:female), a male and a female pupal density is calculated as 67% and 33% of the total pupal density, respectively [IV. B. 1]. Pupae assigned to each sex emerge at a rate determined by the probability density function of percentage emergence as a function of physiological time (T.U.s) [IV. D. 1]. Mortality is considered a constant resulting in the removal of 43% of each daily cohort at emergence [IV. F. 2].

Factors affecting the overwintering success rate of winter color morphs are unknown. In order to complete this subsystem, relationships between indices of moth fitness, environmental pressures, and overwintering success rates must be investigated. Theoretically, those individuals surviving the winter would enter Subsystem I (Figure 19 & 20) at step 1, and the simulation of the population dynamics of A. minuta would begin with the SI generation.

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